FORAGING ECOLOGY OF WINTERING WADING BIRDS ALONG THE GULF OF MEXICO COAST

A Dissertation

by

DAWN ANN SHERRY

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2006

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	R. Douglas Slack
Committee Members,	Felipe Chavez-Ramirez
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ABSTRACT

Foraging Ecology of Wintering Wading Birds

Along the Gulf of Mexico Coast. (December 2006)

Dawn Ann Sherry, B.S., Indiana University of Pennsylvania;

M.S., Indiana University of Pennsylvania

Chair of Advisory Committee: Dr. R. Douglas Slack

I studied flock composition, distribution and foraging ecology of wintering wading birds along the Gulf of Mexico coast. I focused on geographic variability in wintering wading bird assemblages, the processes that structured these assemblages and habitat use by wading birds. I found considerable variation among three sites, Aransas National Wildlife Refuge (ANWR), Texas; Marsh Island Wildlife Refuge (MIWR), Louisiana; and Chassahowitzka National Wildlife Refuge (CNWR), Florida. Species comprising wintering wading bird assemblages varied regionally. ANWR had the most species-rich assemblage, with eight species. MIWR had only six wading bird species. And CNWR had only three different species.

Processes that structured wintering wading bird assemblages also varied regionally. In ANWR, Texas, the Random Fraction niche apportionment model (RF model) best explained the empirical abundance data for ANWR. For abundance data from MIWR a good fit was obtained with the MacArthur Fraction (MF) model and the Power Fraction (PF) models. None of the models fully explained the CNWR abundance data.

I also examined patterns of habitat partitioning among wintering wading birds at three different scales at two sites, Matagorda Island National Wildlife Refuge (MINWR) and Laguna Atascosa National Wildlife Refuge (LANWR). At the macrohabitat level, wintering wading birds showed interspecific differences in macrohabitat use of both open water habitats and vegetated flats. At the mesohabitat level all species at MINWR used the category nearest the edge most

often, alternatively, at LANWR wading birds were most often in the mesohabitat category of 8.1-12 m. from the edge. In both locations wading birds partitioned habitat based on water depth.

Finally, I found that Great Egrets and Snowy Egrets participated more often in flock foraging and derived more benefits from feeding in flocks than other species. Great Egrets feeding in flocks had a higher mean strike rate than those foraging alone, whereas Snowy Egrets had a higher success rate foraging in flocks than those foraging alone. In the case of the darker-colored species (e.g., Great Blue Herons, etc.) they either showed no difference in behaviors between birds foraging in flocks versus those foraging alone or they actually did worse when they foraged in flocks.

DEDICATION

I dedicate this dissertation to my parents, their love and support gave wing to my dreams.

ACKNOWLEDGEMENTS

I would like to thank Felipe Chavez-Ramirez for giving me the opportunity to do this project. Not only was he instrumental in helping me to formulate my ideas, he also was very generous about providing me many opportunities to pursue multiple side projects and for these experiences I am grateful. I would also like to thank Dr. Slack for taking me into the "flock" and helping to shape my growth both as a scientist and as a teacher. I would also like to thank my other committee members, Dr. Fran Gelwick and Dr. Ben Wu for their support, helpful suggestions and ideas.

Probably nobody has done more to help me with field work than Charley Land, who accompanied me on many a trip. I would also like to thank Craig Westwood and Steve Windels who also provided field assistance.

The staff at all of the refuges were generous, accommodating and a downright pleasure to work with, and I would like to thank them for their time. Specifically, at Matagorda Island National Wildlife Refuge, I would like to thank Jennifer Sanchez and Doc and Martha McAllister. Matagorda is a special place and it is so, in part, due to these people. Special thanks to Tim Cooper formerly of Laguna Atascosa NWR, Edmond Mouton at Marsh Island Wildlife Refuge LA, Seth Blitch and Joe Conti at St. Martin's Marsh Island Preserve FL, Bob at Chassahowitzka NWR and James Burnett at St. Mark's NWR in Florida.

I would like to acknowledge the support of the Caesar Kleberg Wildlife Research Institute at Texas A&M University Kingsville and the Department of Wildlife and Fisheries Sciences at Texas A&M University College Station. Both departments provided extensive funding and logistical support for this project. Partial funding was provided by a grant from The Nature Conservancy's Enron Environmental Fellows Program.

Special thanks to my husband Carl. You always believed in me and you always threw the fish trap! To all the good friends that I made in both Kingsville and College Station, thank you all (and you know who you are!) This has been an amazing experience!

Finally, I would like to thank the many people at Macon State College, who supported my efforts to complete this dissertation. Barry, I could not have gotten this through the thesis clerk without your anal retentive ways. We all have our gifts and I am glad you shared yours with me!

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CHAPTER I

INTRODUCTION: OVERVIEW OF WINTERING WADING BIRD ECOLOGY

Conservation and management plans for wading bird assemblages (i.e., herons, egrets, ibis and spoonbills) in North America have focused on the breeding season, despite evidence that the nonbreeding season is important to wading bird populations (Mikuska *et al.* 1998). As nearly all North American heron populations are migratory (Hancock and Kushlan 1984), it is important that key wintering areas are identified and included in management plans (Mikuska *et al.* 1998). Once key areas are identified, further research can be done to determine how specific resources (e.g., roosting sites, habitat, etc.) are important to wintering wading birds.

The Gulf of Mexico coast has been identified as an area supporting significant numbers of wintering wading birds (Mikuska *et al.* 1998). The Texas Gulf coast was identified as a key area for several species including Great Egrets (*Ardea alba*), Reddish Egrets (*Egretta rufescens*) and Tricolored Herons (*Egretta tricolor*). Despite this region's importance to wintering birds, few studies have focused on nonbreeding season foraging ecology along the Texas coast (but see (Chavez-Ramirez and Slack 1995; Dubowy 1996). These studies focused primarily on habitat use patterns and have not examined patterns of food use, prey density or the relative importance of flock foraging.

There are several reasons to expect differences between breeding and nonbreeding seasons in both habitat and food utilization patterns. Fall migrations from temperate latitudes to southern latitudes create an influx of migrants using coastal marshes either as stopover sites or as

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This dissertation style follows Waterbirds.

wintering areas (Coffey 1943; 1948; Dusi and Drozd 1967; Browder 1973; Byrd 1978; Ryder 1978; Hancock and Kushlan 1984). This influx of migrants could cause a shift in habitat use patterns of resident herons or egrets. New arrivals also could affect patterns of food-resource use by impacting prey densities and subsequently changing overall patterns of food-resource use by both resident and over-wintering birds (Kushlan 1978).

Habitat and food utilization patterns also could differ because adults are no longer feeding nestlings in the nonbreeding season. Many nestlings have physiological constraints that dictate the food they can eat, and this influences both habitat and food resource use by adults (Bildstein *et al.* 1990). When adults are no longer feeding nestlings during the nonbreeding season, subsequent changes in habitat and food use patterns could occur.

In addition, changes in environmental parameters (e.g., water temperature, dissolved oxygen, etc.) during the winter alter prey movements or reduce prey availability (Kushlan 1976a; Frederick and Loftus 1993). Wading birds primarily consume fish and will alter patterns of habitat use to track prey (Kushlan 1976a; 1981). Thus, prey movement into and out of marshes during periods of cold weather during the winter season could change prey availability and thus alter habitat and food-use patterns of wading birds.

For management and conservation purposes the number of wading birds of each species and interspecific differences in habitats used for key conservation areas and interspecific differences in their habitat use are needed to identify key conservation areas (Mikuska *et al.* 1998). Knowledge of winter season-foraging ecology also can contribute to an understanding of breeding parameters required by species (Frederick and Bildstein 1992). Better knowledge of the prey base can help to maintain or increase existing populations of wading birds, if resources obtained during the nonbreeding season are found to limit future reproductive success (Martin 1987).

ASSEMBLAGE COMPOSITION

The Gulf of Mexico coastal marshes are important sites for assemblages of wintering wading birds. However, coastal marsh use differs among wading bird species and by geographic locations (Mikuska *et al.* 1998). For example, the Gulf coast in Texas is an important for site for wintering Great Egrets, Reddish Egrets and Tricolored Herons, whereas the Mississippi delta region of the Louisiana coast supports significant numbers of Great Egrets and Tricolored Herons (Mikuska *et al.* 1998). The broad geographic area that the Gulf of Mexico coast covers makes it difficult to conduct detailed studies of all wading bird species in every coastal marsh. Newly developed niche apportionment models can help researchers interested in studying biodiversity to efficiently partition their own limited time and money (Magurran 2004).

There are two types of niche apportionment models, statistical and biological/theoretical models. Statistical models enable an investigator to compare different assemblages. If the goal is to explain rather than merely describe the relative abundances of species in an assemblage, then it is necessary to predict how available niche space might be divided among constituent species and then ask whether the observed species abundances match this prediction. Because there are many different ways in which resources could be subdivided among species, biological/theoretical models represent different scenarios of niche apportionment.

HABITAT UTILIZATION

Habitat partitioning is the first step in resource partitioning by wading birds (Ramo and Busto 1993). Different patterns of habitat partitioning may emerge depending on the scale at which the patterns are examined and these differences may influence conclusions about

underlying processes (Wiens 1981; Levin 1992). During the breeding season, wading birds partition habitat at a variety of scales. At the macrohabitat or landscape scale, different species of wading birds utilize water bodies differing in size (Chavez-Ramirez and Slack 1995) and salinity (Ramo and Busto 1993; Maccarone and Parsons 1994). Interspecific differences in macrohabitat utilization may be due to different types or sizes of prey available among water bodies differing in size, or because of behavioral interactions, such as territoriality, that constrains use of habitats among individuals. At the mesohabitat scale, defined within a water body, as the distance between a bird and land, some species partition habitat across a terrestrial-aquatic gradient (Frederick and Bildstein 1992). At the finest or microhabitat scale, (i.e., location where each bird is standing within a body of water) water depth or tidal level most strongly influences patterns of wading bird habitat use (Meyerriecks 1962; Kushlan 1976b; Custer and Osborn 1978a; Hom 1983; Maccarone and Parsons 1994; Austin 1996; Strong et al. 1997).

Two other factors that impact habitat utilization are vegetation (Jenni 1969; Kushlan 1976b; Custer and Osborn 1978b; Hom 1983) and relative efficiencies of foraging behavior in different habitats (Kushlan 1978b). Patterns of habitat partitioning at any of these scales (macro- meso- or microhabitat) are important when different prey types are found in different habitats, or when habitat type influences the foraging efficiency of individual waders (Kent 1986; 1987).

FLOCK DYNAMICS

An important aspect of wading bird foraging behavior is flock feeding. During both the breeding and nonbreeding season, wading birds are commonly observed feeding in large-sized mixed-species flocks (Kushlan 1976b; Caldwell 1981; Hafner *et al.* 1982; Master 1992; Master

et al. 1993; Smith 1995). Proposed benefits of mixed-flock feeding can be grouped into two broad categories: 1) benefits derived during foraging, i.e., efficient use of clumped or ephemeral resources; gaining information as to the distribution of prey by watching others forage; increased positive social interactions such as commensalisms; increased foraging success or net energy return and 2) anti-predator benefits (Moynihan 1962; Turner 1964; Morse 1970; Cody 1971; Ward and Zahavi 1972; Krebs 1974; Cezilly *et al.* 1990; Master 1992; Master *et al.* 1993).

Benefits of flock foraging by wading birds may vary by species due to plumage color. Species most commonly observed in the center of foraging flocks (e.g., Snowy Egrets (*Egretta thula*), Great Egrets, and Roseate Spoonbills, (*Ajaia ajaia*) tend to have lighter-colored plumage than those feeding peripherally (e.g., Great Blue Herons (*Ardea herodias*), Little Blue Herons (*Egretta caerulea*), Tricolored Herons, etc.) (Kushlan 1978; Master 1992; Master *et al.* 1993). Juvenile Little Blue Herons, which have white plumage, are attacked less often and catch more fish than dark-plumaged adults in mixed species foraging flocks (Caldwell 1981). Light juvenile plumages may have evolved to take advantage of an increase in energy gain while foraging in mixed-species flocks (Caldwell 1981).

Species specific foraging behaviors also may negatively affect individual foraging success of birds in a flock. Species that utilize highly active foraging behavior (e.g., Reddish Egrets) have increased agonistic interactions when foraging in a flock (Kushlan 1978). Likewise, species that methodically search may capture fewer prey while foraging in a flock due to disturbance created by other more active species (Kushlan 1978). Species at the core of feeding aggregations tend to feed either while standing in place, e.g., Snowy Egrets or Great Egrets (Caldwell 1980; 1981; Master 1992; Master *et al.* 1993) or by slow tactile feeding, as in Roseate Spoonbills or ibises (*Eudocimus* or *Plegadis*, *spp*.) rather than by active behaviors such as disturb-and-chase used by Reddish Egrets (Kushlan 1978). Additional costs associated with

flock foraging include interference and other negative social interactions, such as prey robbing (kleptoparasitism). Prey robbing has been reported in several species of wading birds and it can occur both intra and interspecifically (Kushlan 1978; Amat and Rilla 1994).

The goal of this research is to examine the foraging ecology of wintering wading birds in in habitats of key conservation areas already established along the Gulf Coast of Mexico. Specifically, in chapter II, I examine and compare patterns of wading bird community assembly in three regions along the Gulf of Mexico coast. In chapter III, I examine conspecific and heterospecific patterns of habitat partitioning in these same three regions. In chapter IV, I compare patterns of habitat utilization at three landscape levels, macrohabitat, mesohabitat and microhabitat among two salt marshes in Texas. In chapter V, I investigate the influence of mixed-species foraging aggregations on behavior, foraging success and energy expenditure by comparing individuals within flocks to solitary individuals.

CHAPTER II

ASSEMBLAGE COMPOSITION AND NICHE APPORTIONMENT OF WINTERING WADING BIRDS IN THREE DIFFERENT REGIONS ALONG THE GULF OF MEXICO COAST

SYNOPSIS

I used niche apportionment models to predict how available niche space is divided among assemblages of wintering wading birds and in addition, I asked whether the observed species abundances match this expectation. I compared patterns of species evenness in wading bird assemblages among three regions of the Gulf of Mexico coast. Variability in species abundances among different assemblages can define and distinguish between different assemblages and can give insight into the processes that helped to shape an assemblage. I conducted flights on a fixed-wing aircraft to count wading birds but not to measure densities. I conducted three flights over Aransas National Wildlife Refuge (ANWR), Texas, two flights over Marsh Island Wildlife Refuge (MIWR), Louisiana and three flights over Chassahowitzka National Wildlife Refuge (CNWR), Florida to determine number of individuals of wading bird species. I used the PowerNiche program to test the fit of my abundance data from each region to each of three theoretical models, the Power fraction model (PF), the Random fraction model (RF), and the MacArthur Fraction Model (MF). These models represented different scenarios of niche apportionment. Niche apportionment models fit empirical data completely in only one location, ANWR. The RF model fitted data well for ANWR, with all the observed species abundance values lying inside the 95% C.I. This implies that resources were not limited in

ANWR and there was high niche overlap between existing species in the assemblage and invading species in regards to resource use (e.g., food type and/or habitat type). Perhaps this is due to the strong influence weather has on both the habitat and the food resources in the coastal marshes of Texas. For both MIWR and CNWR, when niche apportionment models were compared to empirical data, both locations had at least one observed species abundance value falling outside of the 95% C.I. for all three models. Explanations for the lack of a clear pattern include a need for more flights or perhaps processes different than those accounted for in the models are operating.

INTRODUCTION

The Gulf of Mexico coast is an important site for assemblages of wintering wading birds. However, coastal marsh use differs among both wading bird species and geographic locations (Mikuska *et al.* 1998). For example, the Texas Gulf coast is an important site for wintering Great Egrets, Reddish Egrets and Tricolored Herons, whereas the Mississippi delta region of the Louisiana coast supports significant numbers of Great Egrets and Tricolored Herons (Mikuska *et al.* 1998). The geographical area of the Gulf of Mexico coast makes it difficult to conduct detailed studies of all wading bird species in every coastal marsh. Time and money are limited, sampling is often patchy and these problems are magnified as the inaccessibility of habitat and scale of the investigation increases (Magurran 2004). In short, ecological investigations are molded by their geographic scale. Heightened interest in biodiversity issues has led to the development of new measurement techniques. New niche apportionment models are one such technique (Magurran 2004). Where the totality of a resource divided by an assemblage of species is assumed to be more or less fixed in quantity, the term

niche apportionment model is used in preference to the more general niche-oriented models (Tokeshi 1990).

There are two main types of niche apportionment models, statistical and biological or theoretical models. Statistical models have the advantage of enabling an investigator to objectively compare different assemblages. If the goal, however, is to explain rather than merely describe the relative abundances of species in an assemblage, then it is necessary to predict how available niche space might be divided amongst the constituent species and then ask whether the observed species abundances match this prediction. Because there are many different ways in which resources could be subdivided among species, biological/theoretical models represent different scenarios of niche apportionment. For example, the dominance pre-emption model (Tokeshi 1990) envisages a situation where the niche space of the least abundant species in an assemblage is invariably invaded by colonizing species. In contrast the dominance decay model the niche of the numerically predominant (i.e., most abundant) species is targeted. The dominance pre-emption process generates a very uneven assemblage in which status of the most abundant species is preserved while the least abundant species lose resources and become progressively rarer over time. In contrast, the dominance decay model produces a very even community (Tokeshi 1990).

The objective of this research was to compare patterns of species evenness in wading bird assemblages among three regions of the Gulf of Mexico coast. Patterns of species evenness, or the variability in species abundances within different assemblages can define and distinguish between different assemblages. More importantly, examining species evenness can give insight into the processes that helped to shape an assemblage. Assemblages with a small number of taxonomically related species are amenable to a more meaningful analysis in terms of species-abundance patterns and the mechanisms underlying them (Tokeshi 1990; 1992; 1996). Niche

orientated models may hold more relevance for these types of assemblages, making wintering wading bird assemblages well-suited for niche apportionment models. The underlying assumption is that the abundance of a species, in part, reflects its success at competing for limited resources. No assemblage has unlimited resources and there are always one or more factors that set the upper limit to the number of individuals and ultimately, the number of species that can be supported. As new species enter into the assemblage, the niche is divided or apportioned among the new species. Thus the differences in relative abundances of species in an assemblage may be a reflection of niche apportionment, in other words, the abundance of a species is assumed to correspond directly to the amount of niche apportioned to that species (Magurran 2004).

METHODS

Study Areas

I compared patterns of species evenness in wading bird assemblages among three regions of the Gulf of Mexico coast. The first region was represented by Aransas National Wildlife Refuge (ANWR), located in the coastal bend region of Texas, Calhoun County (Fig. 2.1). The salt marsh areas were located on the eastern coast of the refuge along Blackjack peninsula and consisted of vegetated flats dominated by glasswort (*Salicornia virginiana*), saltwort (*Batis maritima*), sea-oxeye daisy (*Borrichia frutescens*), wolfberry (*Lycium carolinianum*), saltgrass (*Distichlis spicata*), smooth cordgrass (*Spartina alterniflora*), and wind tidal flats dominated by mudflat grass (*Eleocharis parvula*) saltgrass and cordgrasses.

Interspersed among vegetated areas were bodies of open-water of varying sizes (Chavez-Ramirez and Slack 1995).

The second region was Marsh Island Wildlife Refuge and Game Preserve (MIWR), located off the southern coast of Louisiana between Vermillion Bay and the Gulf of Mexico (Fig 2.2). Prominent marsh vegetation included wire grass (*Spartina patens*), three corner grass (*Scirpus americanus*), and black needle rush (*Juncus roemerianus*). Shrub species such as salt bush (*Baccaris halimifolia*) and marsh elder (*Iva frutescens*) occurred along spoil banks. There were also several tree species including: hackberry (*Celtis laevigata*), Chinese tallow (*Sapium sebiferum*), chinaberry (*Melia asedrarach*), Toothache tree (*Zanthoxylum clava-herculis*) and Huisache (*Acacia farnesiana*).

The region in Florida was represented by a study site encompassing two adjacent areas (Fig. 2.3), the St. Martin's Marsh Aquatic Preserve (SMMAP), which is located in Citrus county and the Chassahowitzka National Wildlife Refuge (CNWR), which is located in both Citrus and Hernando counties. Both CNWR and the adjacent Preserve were composed of open water, inlet bays, tidal rivers and creeks, and salt marsh. The major plant community associations found here included salt marsh, tidal flats, marine grassbeds, mangrove forest and hammock islands. The majority of my research was conducted in the salt marsh areas. The dominant plant species here are black needle rush (*Juncus roemerianus*), salt grass and smooth cordgrass. Additionally, there were many areas of marine grassbeds, vegetated by such grasses as turtle grass (*Thalassia tetudinum*) and shoalgrass (*Halodule wrightii* and *Ruppia maritima*). The water in these areas was known for its high clarity (St. Martins Marsh Aquatic Preserve Management Plan. Department of Natural Resources. September 9, 1987).

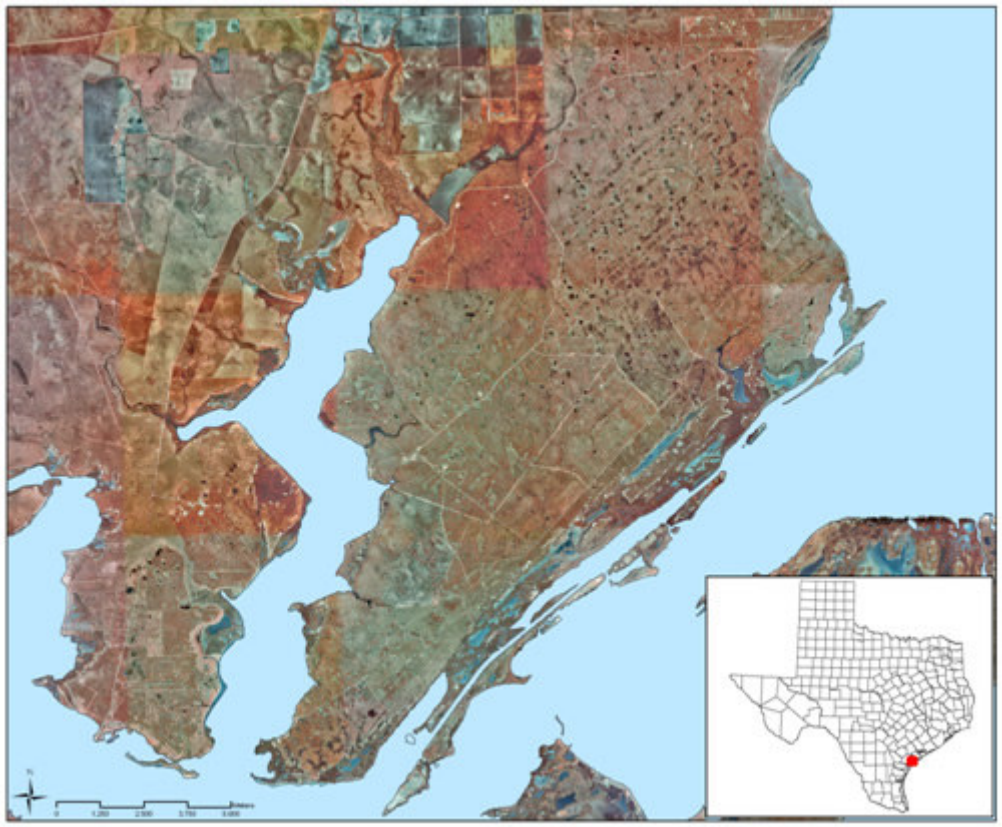


Figure 2.1. Aransas National Wildlife Refuge (ANWR), Texas.

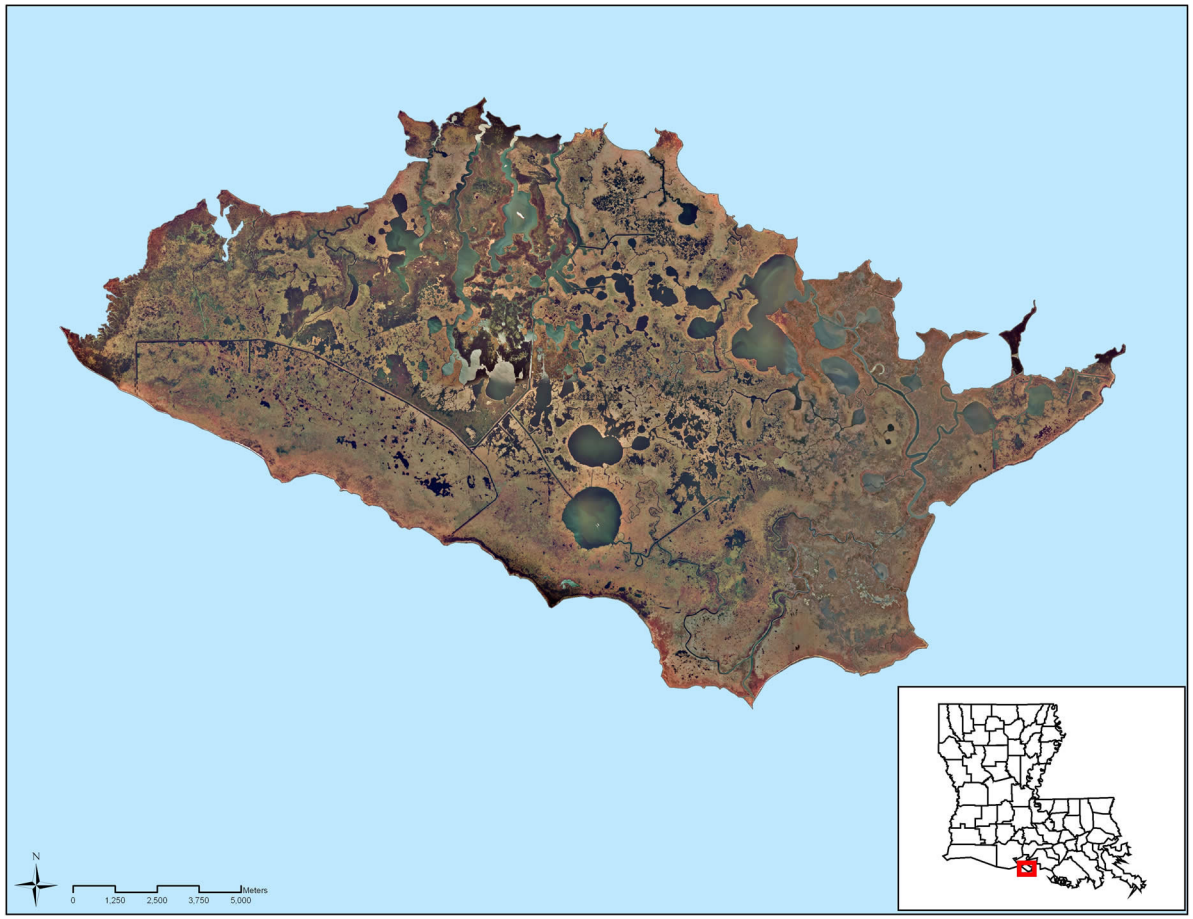
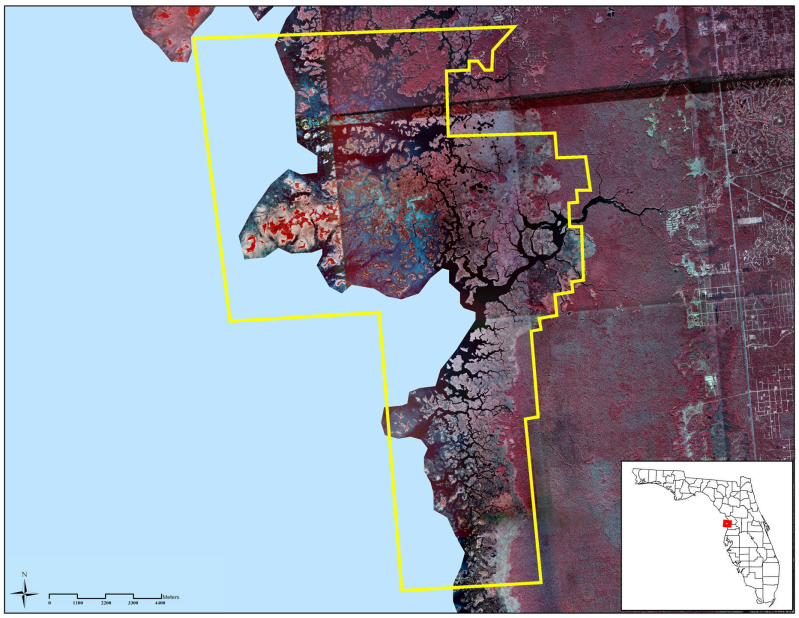


Figure 2.2. Marsh Island Wildlife Refuge (MIWR), Louisiana.

A



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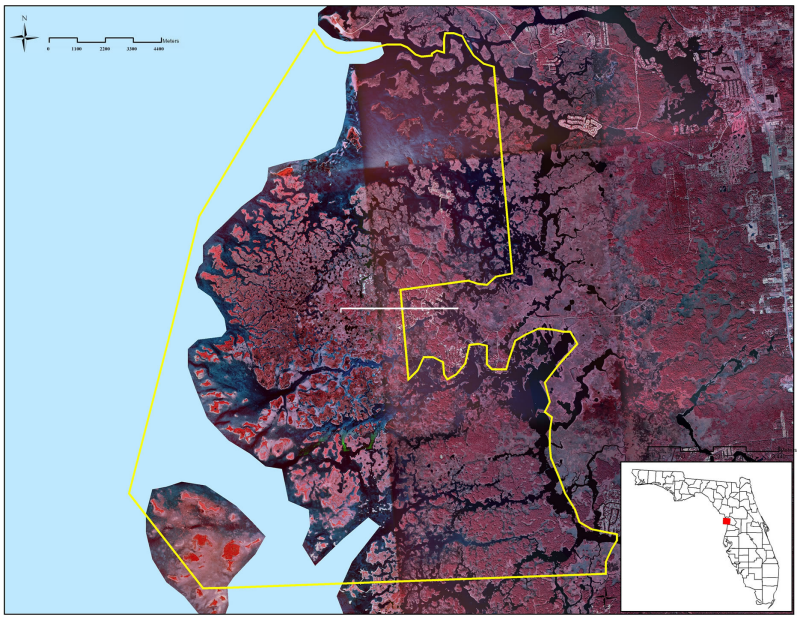

Figure 2.3 A) Chassahowitzka National Wildlife Refuge (CNWR) and B) St. Martin's Marsh Aquatic Preserve (SMMAP), Florida.

Flights

At ANWR observations of wading bird habitat use were made from a fixed-wing aircraft from 12 December 1996 through 31 December 1996. A total of 3 flights were conducted. During each flight, transects were flown parallel to the coastline at an altitude between 30 and 50 m. A linear distance of approximately 175 km was covered on each flight. The first transect was flown along the coast with successive transects approximately 0.5 km inland from the previous one. Due to the large abundance of wading birds present in the marshes, only wading birds observed within 25 m perpendicular to the flight line on the observer's side of the aircraft were identified and counted. Birds not identified to species were eliminated from the analysis. I conducted two flights over MIWR, Louisiana and three flights over CNWR/SMMAP, Florida to determine distribution and abundance of wading birds. Inclement weather events prevented more aerial surveys at these sites.

Each survey of MIWR consisted of fourteen flight lines, approximately 1.6 km apart (east to west), flown in a north to south direction for a total linear distance of 135 km flown during each survey. Transects in MIWR were conducted on 5 December 1997 and 13 February 1998, respectively. Five flight lines approximately 1.62 km apart (east to west) were flown over CNWR/ SMMAP from north to south, for a total linear distance flown of 60 km per survey. Flights were conducted in Florida during 21 January, 20 February, and 1 April, 1998, respectively. Flights to observe wading birds were conducted along lines between 30.5 and 61 meters apart in order to locate and identify species more easily. Due to flying restrictions in Florida, surveys could not be conducted below 152.4 meters, which made locating and differentiating Tricolored and Little Blue Herons difficult; therefore neither species was tallied at this site.

Flights were focused on locating the following species of wading birds: Great Blue Herons, Great Egrets, Snowy Egrets, Little Blue Herons, Reddish Egrets, Tricolored Herons, Roseate Spoonbills and White Ibises, (with the exception of Tricolored and Little Blue Herons in Florida aerial surveys). Within all three regions the landscapes flown had similarities in landscape elements consisting of open water and vegetated patches of variable sizes. I recorded individual birds, and bird species.

Rank-Abundance Plots

To highlight differences in evenness among wading bird assemblages in ANWR, TX, MIWR, LA and CNWR, FL, I used rank-abundance plots (Magurran 2004). I plotted species in sequence from most to least abundant along the horizontal axis with their abundances displayed in a $\log_{10}$ scale on the vertical axis.

Niche Apportionment Models

I used the PowerNiche program (Drozd and Notovny 1999) to test the fit of three theoretical models with abundance data (number of individuals) from three locations (ANWR, Texas; MIWR, Louisiana; and CNWR, Florida). The models that I tested were the Power fraction model (PF), the Random fraction model (RF), and the MacArthur Fraction Model (MF) (Tokeshi 1990; 1996a). These models represented different scenarios of niche apportionment. All of the models made the assumption that the fraction of niche space occupied by a species is proportional to its abundance and that niche space is sequentially divided among species as they join the assemblage. In all cases the models assume that the target niche–the one selected for

division–is divided at random. The differences between the models lie in the way in which the target niche is selected. (Tokeshi 1990; 1992; 1996a; Magurran 2004).

The models are classified according to the probability that the largest niche (i.e., the most abundant species) in an assemblage is chosen for subsequent division. In the RF model, the probability is 0. In other words, a new invading species randomly selects one of the existing species' niches and gets a random fraction of it. All of the existing species have the same probability of being selected for a subsequent niche division, i.e., the current abundance or niche size does not affect the chance that species is challenged by an invading species. The RF model is analogous to a situation in which a new, invading species randomly selects one of the existing species and gets a random fraction of its niche, i.e., there is no dominance hierarchy in this model (Tokeshi 1990; 1996a; 1996b). In the MF model, all species in an assemblage are subject to invasion by a new species, with the probability of invasion being dependent on the abundance or niche size of each species. The MF model postulates that a new species is more likely to invade the niche space of a more abundant species and gets an arbitrary fraction of it. There is no a priori information on superiority/inferiority (Tokeshi 1990). Thus a species with a higher abundance is more likely to experience niche fragmentation than a less abundant one. In the PF model, the probability of selection is proportional to niche size (or abundance) raised to a power exponent k ($0 \leq k \leq 1$). The PF model envisages a scenario in which assemblages may be formed by a sequential niche apportionment process where the probability of successive niche division tends to be higher (but only slightly so) for species with larger niches/higher abundances.

In the PF model (Tokeshi 1996a), a line representing the resource unit is divided into two segments at random, and in each next step, one of the segments is chosen and divided at random again, until N segments are obtained. The probability of an i-th segment being selected for division is $p_i = ax_i^k$, where a is a constant ($\sum ax_i^k = 1$), x_i is the length of the segment and k is a

parameter of the model. The point of division of the i-th segment, delimited by the x_{imin} and x_{imax} bounds on the resource unit line, is determined as $x_{imin} + 0.5\ x_i z$, where z is a random number drawn from a uniform (0, 1) distribution. The length of the larger of the two segments created by this division can be any value from 0.5 to 1.0 with equal probability, so that its average length is 0.75. In the power PF model, the probability that a niche will be split is positively related to its size through a power function k (that is x^k where k ranges from 0 to 1). As k approaches 1, it becomes more likely that the largest niche will be selected for fragmentation. Indeed, when k = 1 the PF model resembles the MF model (in which larger niches have a greater probability of fragmenting). Conversely, when k = 0, a completely random choice of niche fragment is restored and the model corresponds to the RF model (Drozd and Notovny 1999; Magurran 2004).

I compared wading bird species assemblages from ANWR to each of the models by running 250 simulations to create a total of 250, eight-species assemblages. For MIWR I created 250, six species assemblages and for CNWR I created 250, three-species assemblages, reflecting the number of different species detected during flights in different locations. Using these 'parent populations' 95% confidence intervals were derived for the mean abundances of the first to the last ranking species, i.e., these confidence intervals indicated a range of values of mean abundance for each rank likely to be encountered if a small sample were randomly drawn from the parent population and mean abundance calculated on the basis of this small sample. With μ_i and σ_i denoting, respectively, mean and standard deviation of the abundance of the i^{th} rank in the parent population, the mean abundance value $\overline{x_i}$ from a sample of size n was expected to lie within

$$\text{Confidence Interval} = \mu \pm \frac{r\sigma}{\sqrt{n}}$$

where $r = 1.96$ for 95% confidence limits. I compared these theoretical values with the observed mean abundances derived from the data sets. If the observed values for the first to the last rank fell within the corresponding confidence interval from theory, the observed pattern of species abundance was judged to be in conformity with the model's expectation (Tokeshi 1996b; Magurran 2004). Finally, I superimposed the mean observed abundances (i.e., flight data) on a graph showing the mean (± confidence interval) of the expected values (i.e., those predicted by the models). If there was agreement between the observed data and the pattern predicted by the model, this implied that the niches that the species occupied may indeed be subdivided to the scenario envisaged.

RESULTS

Contrasting patterns of species richness were evident when I plotted rank-abundance for each of the three regions. A total of eight species were observed at ANWR (Table 2.1).

Great Egrets made up the largest percentage of the wading bird assemblage. White Ibis, Snowy Egrets, Roseate Spoonbills, Great Blue Herons, Reddish Egrets, Tricolored Herons and Little Blue Herons were all observed at ANWR, making it the most species rich assemblage I surveyed. Compared to the other regions, ANWR had a relatively even wading bird assemblage (Fig. 2.4). At MIWR, I observed six species (Table 2.2). Snowy Egrets, Roseate Spoonbills and Great Egrets each made up nearly one-third of the assemblage. Other species that were also observed were Great Blue Herons, Tricolored Herons and Little Blue Herons. The rank-abundance curve was relatively flat for the first three species, then dropped off rapidly for the last three species (Fig. 2.5). At CNWR, I only observed three species (Table 2.3). Great Egrets were the dominant species in the assemblage making up 88% of the individuals observed. White Ibis and Great Blue Herons were the only other species observed, making up 7.6% and 4.4% of the wading bird assemblage respectively. The rank-abundance curve for CNWR was quite different from the other two sites because of the high predominance of Great Egrets in the assemblage (Fig. 2.6).

Table 2.1. Number of individuals, percent of individuals and rank of species from greatest to least proportion of the wading bird assemblage observed during flights over ANWR, Texas during the winter of 1996.

Species	Number Individuals	Percent	Rank
Great Egret	1091	35.2	1
White Ibis	856	27.6	2
Snowy Egret	460	14.8	3
Roseate Spoonbill	433	14.0	4
Great Blue Heron	133	4.3	5
Reddish Egret	75	2.4	6
Tricolored Heron	50	1.6	7
Little Blue Heron	5	0.2	8
TOTAL	**3103**	**100.0**	

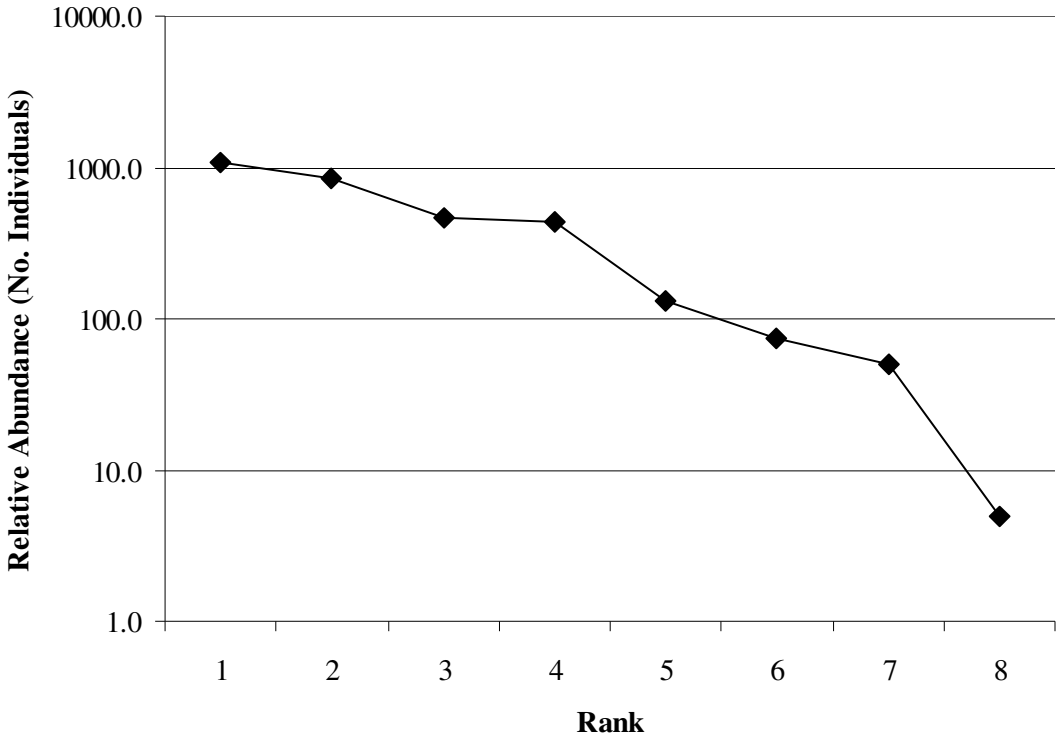

Figure 2.4. Rank-abundance plot of wading bird assemblage observed during flights over ANWR, Texas during December 1998.

Table 2.2. Number of individuals, percent of individuals and rank of species from greatest to least proportion of the wading bird assemblage observed during flights over MIWR, Louisiana during the winter of 1997-1998.

Species	Number Individuals	Percent	Rank
Snowy Egrets	112	29.9	1
Roseate Spoonbills	110	29.4	2
Great Egrets	101	27.0	3
Great Blue Herons	45	12.0	4
Tricolored Herons	5	1.3	5
Little Blue Herons	1	0.3	6
TOTAL	**374**	**100.0**	

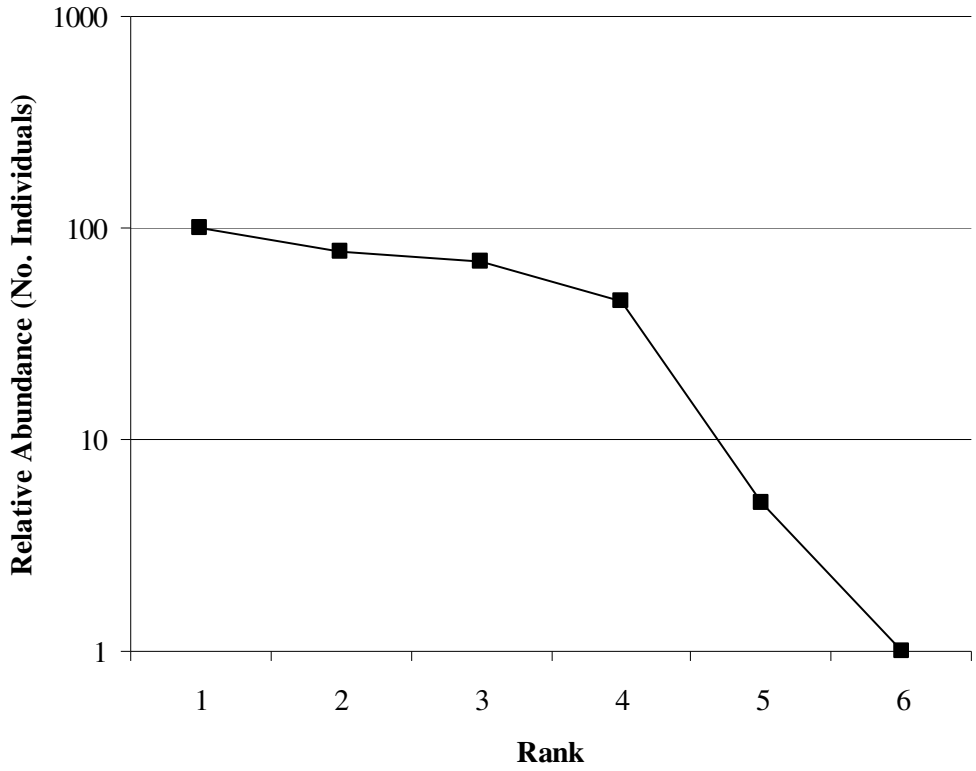

Figure 2.5. Rank-abundance plot of wading bird assemblage observed during flights over MIWR, Louisiana during winter of 1997-98.

Table 2.3. Number of individuals, percent of individuals and rank of species from greatest to least proportion of the wading bird assemblage observed during flights over CNWR, Florida during the winter of 1997-1998.

Species	Number Individuals	Percent	Rank
Great Egret	338	88.0	1
White Ibis	29	7.6	2
Great Blue Heron	17	4.4	3
TOTAL	**384**	**100.0**	

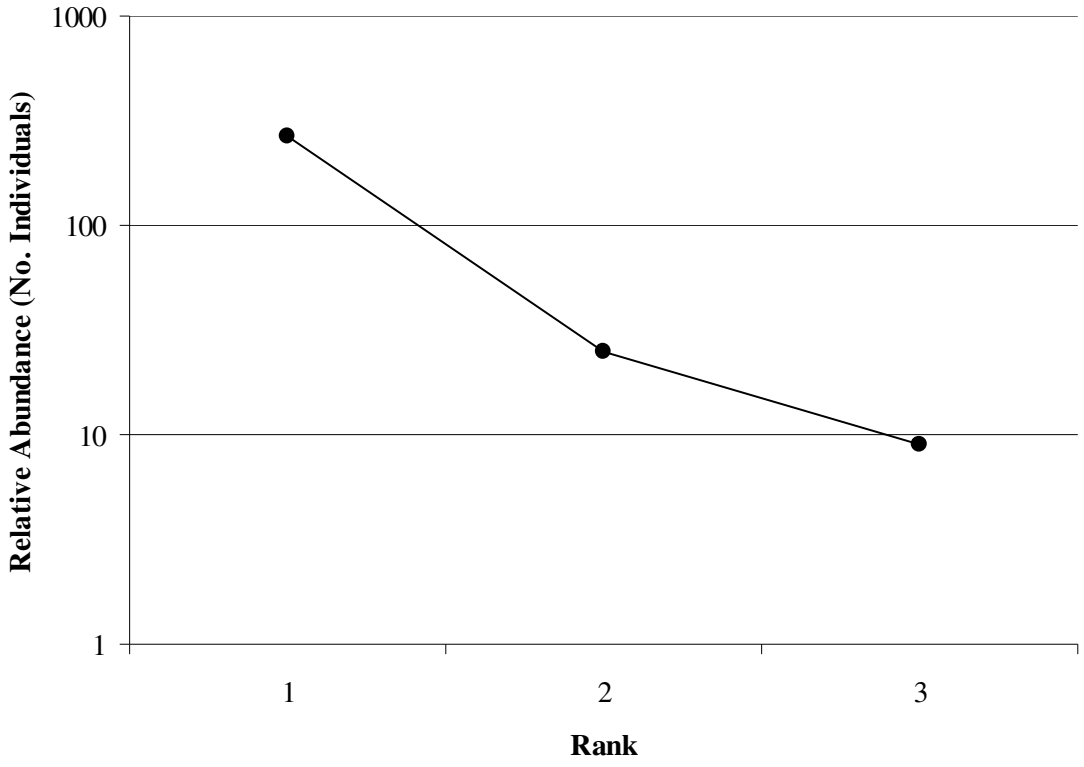

Figure 2.6. Rank-abundance plot of wading bird assemblage observed during flights over CNWR, Florida during winter of 1997-98.

Species-Abundance Patterns

Observed species-abundance patterns in terms of number of individuals for ANWR together with three theoretical patterns are shown in Fig. 2.7. The RF model provided the best fit for the data with all the observed species abundance values lying inside the 95% C.I. Only one of the observed values (the first rank) fell outside the 95% C.I. for the PF model. For the MF model, four out of eight species abundance values (first, fifth, seventh and the eighth ranks) fell outside the 95% C.I. Thus the model cannot be considered to explain the observed pattern successfully. The observed species-abundance data from MIWR showed a different pattern (Fig. 2.8). None of the models was able to predict the empirical data entirely. The MF model and the PFmodel (with $k = 0.5$) each had one observed species abundance value (the third rank) falling outside of the 95% C.I. And for the RF model three out of six species values (third, fourth and fifth ranks) fell outside of the 95% C.I. For CNWR the PF model did not successfully explain the pattern; two out of the three observations (the first and third) fell outside the 95% C.I. Fig. 2.9). Both the RF model and the MF models were more successful in explaining the pattern in that only one of the observations (the first) fell outside the 95% C.I. however, none of the models were successful in explaining species assemblage patterns at CNWR.

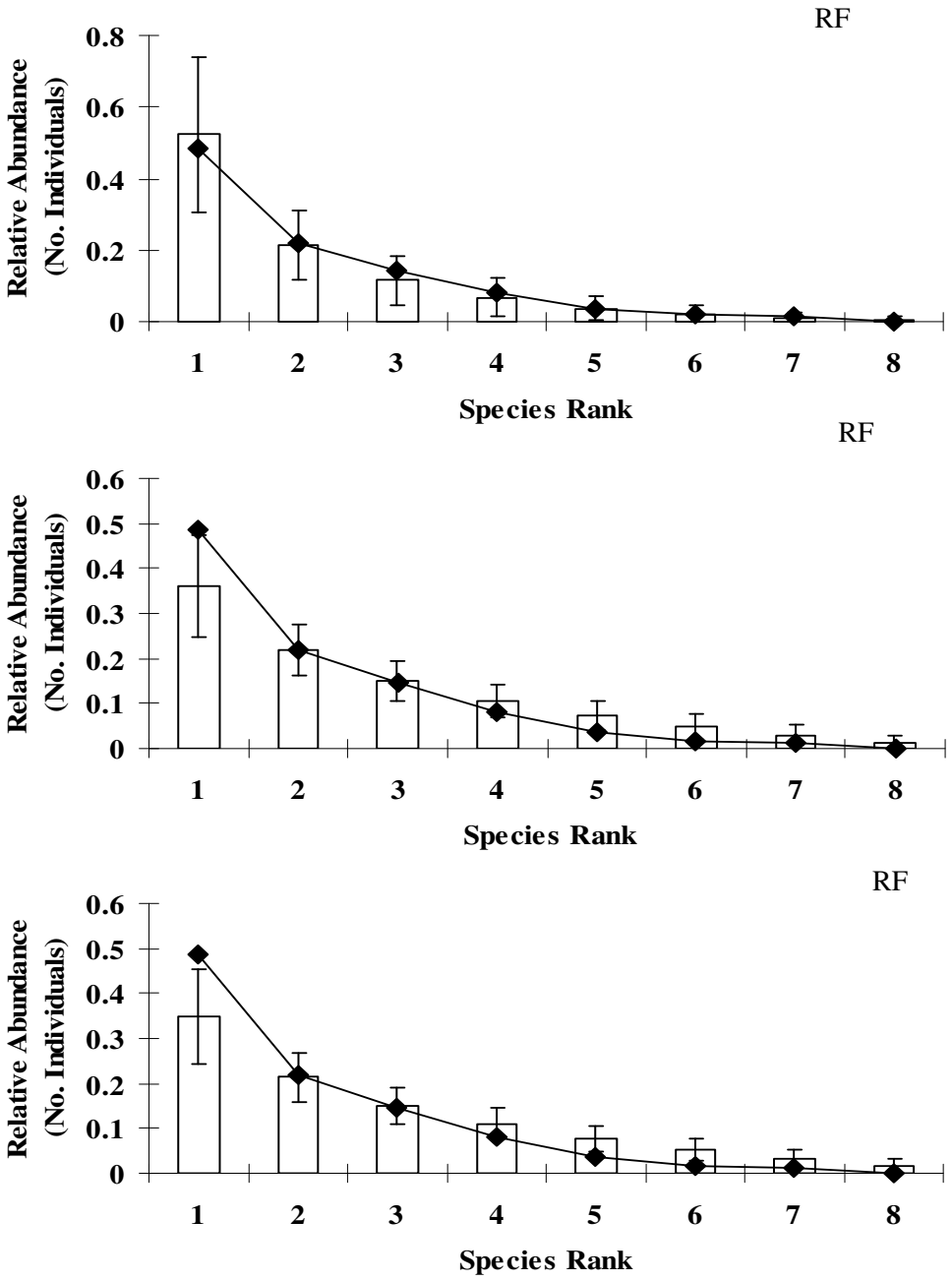

Figure 2.7. Patterns of relative abundance derived from three different models (shown as histograms) compared with observed pattern (■ data from ANWR, TX). RF, Random Fraction model; PF, Power Fraction model; MF, MacArthur Fraction model. Vertical lines associated with histograms are 95% CI for mean abundance values predicted by the models.

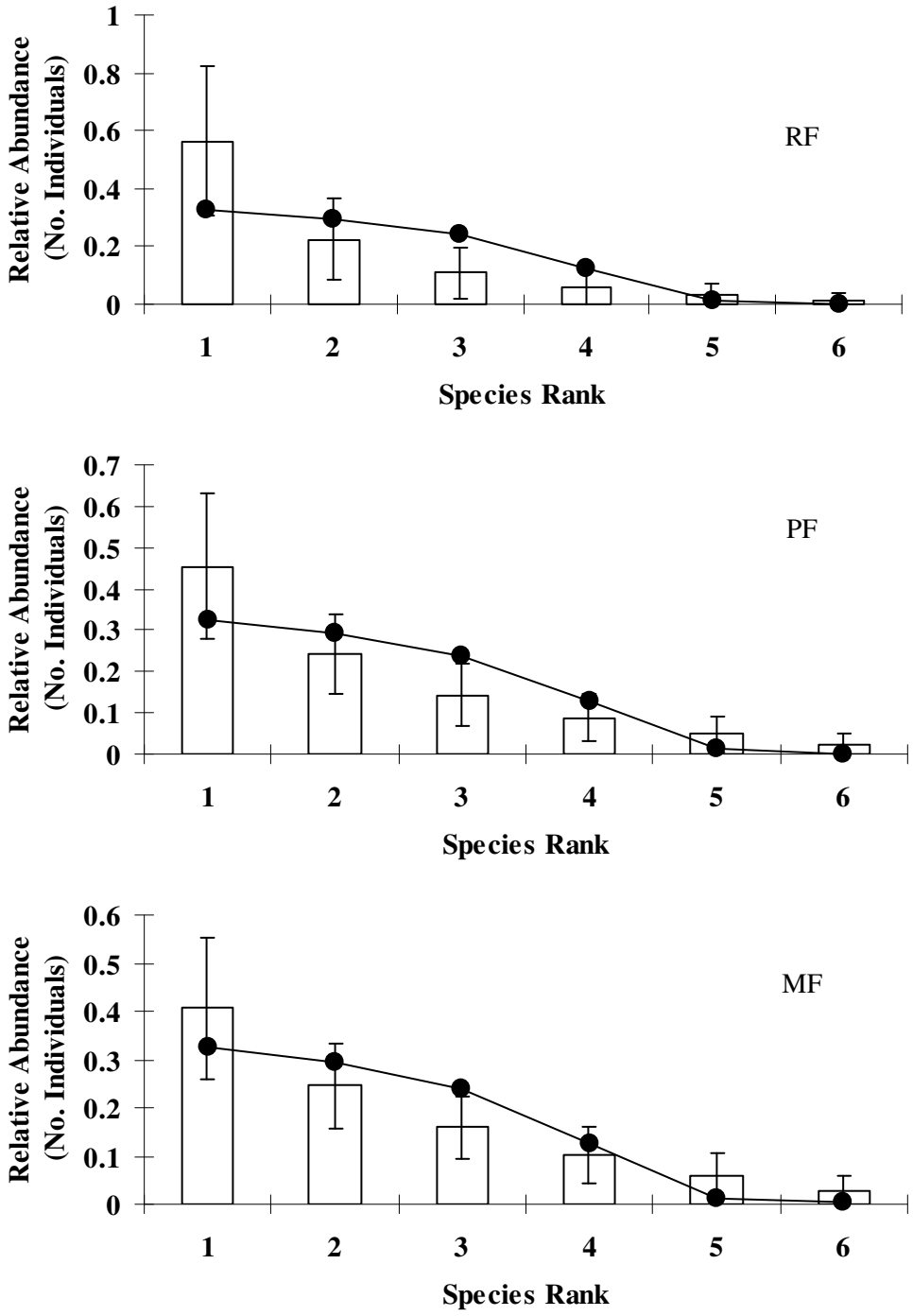

Figure 2.8. Patterns of relative abundance derived from three different models (shown as histograms) compared with observed pattern (● data from MIWR, LA). RF, Random Fraction model; PF, Power Fraction model; MF, MacArthur Fraction model. Vertical lines associated with histograms are 95% CI for mean abundance values predicted by the models.

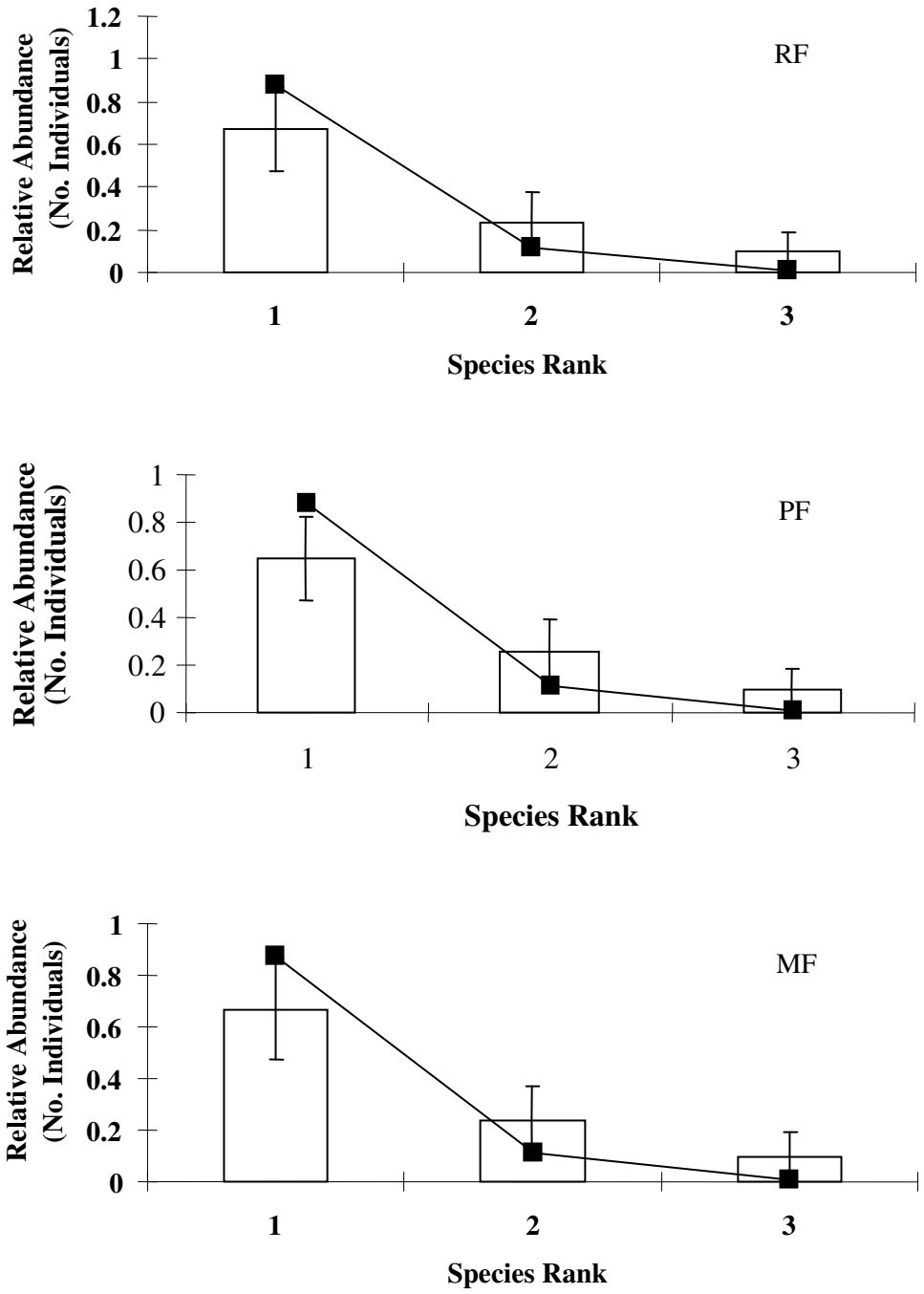

Figure 2.9. Patterns of relative abundance derived from three different models (shown as histograms) compared with observed pattern (data from CNWR, FL). RF, Random Fraction model; PF, Power Fraction model; MF, MacArthur Fraction model. Vertical lines associated with histograms are 95% CI for mean abundance values predicted by the models.

DISCUSSION

The random fraction model (Tokeshi 1990) best fit the empirical data from ANWR. This fit implies that as the wading bird assemblage formed at ANWR, there was no dominance hierarchy among individual wading bird species. Each new invading species obtained a random proportion of an existing species' niche, i.e., resources were not limited in ANWR and there was high niche overlap between invading species and existing species in regards to resource use (e.g., food type and/or habitat type). If resources were limited, one might expect to see evidence of competition. However, at ANWR, there was no evidence of competition among wading birds. Wading birds were never observed staking out territories, rather they often fed in large flocks (D. Sherry pers.obsv.) implying that resources were available in high concentrations locally.

Perhaps the reason that no single species was able to appropriate a large proportion of the niche is due to the strong influence weather has on both the habitat and the food resources in the coastal marshes of Texas. Although there are cyclical tides in the coastal marshes of the GOM, water depth and tidal amplitude are strongly driven by wind direction which is more important than tides and river discharge in creating circulating currents of Texas bays (Britton and Morton 1989). Generally currents flow in the direction of existing wind and localized countercurrent eddies commonly form near shore. During the winter, when northerly winter winds blew, water was pushed to the south sides of the bays, covering north and central Texas barrier island bay-shore marshes with waters as much as 0.5 meter above normal. This seiche effect also forces water and sediments through the tidal inlets. The prevailing southeasterly winds move bay waters in the opposite direction, against the mainland and away from the inner barrier island shores. Southerly winds usually blow more gently, so the seiche effect is less

pronounced (Britton and Morton 1989). At ANWR, winds from the north pushed water into the marsh, raising the water depth and making prey fish less vulnerable to wading bird predation. Conversely, southerly winds pushed water out of the marshes reducing overall water depths and concentrating fish. Wind direction and the weather that drives it are inherently stochastic, and perhaps wintering wading bird assemblages reflect this in that no one species is able to appropriate a large proportion of the niche, due to changing water depths. Water depth is an important factor in habitat partitioning for wading birds in many locales. (Meyerriecks 1962; Kushlan 1976a; Custer and Osborn 1978a; Hom 1983; Maccarone and Parsons 1994; Austin 1996). As water depth at ANWR was closely tied to wind, this introduced more stochasticity into the processes structuring the assemblage.

Circumstantial evidence for the importance of weather events in limiting wading bird populations during the non-breeding season comes from research done in Europe. Specifically, winter droughts in western Africa had significant negative effects on heron populations in Europe (den Held 1981; Cave 1983). The numbers of Purple Herons (*Ardea purpurea L.*) nesting in the Netherlands over a 19-year period and their annual survival rates were correlated with wetland conditions. Low rainfall in western Africa, lowers food supplies on the wintering grounds, which in turn leads to low winter survival and thus a lower breeding population (Newton 2004). A similar relationship was apparent among Night Herons (*Nycticorax nycticorax*) and to a lesser extent Squacco Herons (*Ardeola ralloides*) in the same localities (Cave 1983).

Although ANWR marshes were not subjected to drought conditions like those in the Sahel of Africa, wind direction and rainfall do fluctuate during the winter season. As “northers” blow through the marshes, water levels can change widely and because fish presence is tied to water levels, fish presence is indirectly tied to wind direction. Temperature also affects fish

movements into and out of coastal marshes (Frederick and Loftus 1993). "Northers" blowing through often bring colder air temperatures, which reduce water temperatures. Thus, in addition to lower water depths, fish move to deeper and warmer water when northers blow through, making them less accessible to wading bird predation. The relative stochasticity of these types of weather events and wind direction could have kept this wading bird assemblage from being structured by anything other than random chance, and this in turn may explain why ANWR's wading bird assemblage fits the MF model so well.

In both MIWR and CNWR the models did not adequately explain the data. One reason for lack of congruence with theoretical models could be that these regions are not as strongly influenced by weather patterns. MIWR being located relatively close to the Mississippi river is probably more influenced by river discharge than by wind or lunar driven tidal cycles whereas CNWR was probably more influenced by lunar tidal cycles. These types of events may be more predictable and thus the RF model would be less likely to predict species assemblages here.

CHAPTER III

LANDSCAPE PATTERNS OF HABITAT USE BY WINTERING WADING BIRDS IN DIFFERENT REGIONS ALONG THE GULF OF MEXICO COAST

SYNOPSIS

Although the Gulf of Mexico coast has been identified as a region supporting large numbers of wintering wading birds, there is currently little information on landscape habitat use patterns by these birds during the nonbreeding season. I examined habitat use patterns of wintering wading birds in three coastal marshes of the Gulf of Mexico. Specifically, I compared interspecific patterns of open-water habitat use by wintering wading birds among coastal marshes in Marsh Island Wildlife Refuge (MIWR), Louisiana, Chassahowitzka National Wildlife Refuge (CNWR), Florida and Aransas National Wildlife Refuge (ANWR), Texas using chi-square tests. Next, I compared interspecific patterns of open water habitat use by wintering wading birds within each region. Finally, I calculated niche overlap using Pianka's niche overlap index for each pair of species within each region. Patterns of wintering wading bird habitat use were significantly different among regions ($\chi^2 = 2623.9$, $p < .001$). At ANWR, I observed wading birds most often in ponds, vegetated areas and lakes. At MIWR, I observed wading birds most often in pools, cuts, lakes and ponds. At CNWR, wading bird patterns of habitat use were different compared to the other locations. Wading birds were observed most frequently using inlets and bays. Variation in patterns among regions may be due to wading birds either selecting habitats based on prey availability or selecting habitats based on the availability of the habitats themselves. Within each region patterns of wading bird habitat use were also

significantly different among species. At ANWR habitat use varied significantly among species ($\chi^2 = 1557.2$, $p < .001$). All species used ponds, lakes and vegetated areas more often than expected. Habitat use was significantly different among wading bird species at MIWR ($\chi^2 = 99.3$, $df = 18$, $p < .001$). All species used cuts, bays and ponds more often than expected, whereas they used lakes, inlets and vegetated areas less often than expected. Habitat use was also significantly different for wading birds in Florida ($\chi^2 = 286.9$, $df = 10$, $p < .001$). Niche overlap was highest for Great Egrets and Great Blue Herons in all regions. For these two species, prey type and size seem to be important mechanisms of resource partitioning.

INTRODUCTION

The Gulf of Mexico coast and more specifically regions along the Texas coast and the Mississippi delta have been identified as key areas for wintering North American herons (Mikuska *et al.* 1998). Despite this region's importance, relatively few studies have focused on patterns of habitat use by sympatric wading birds. Current information is lacking on habitat use and abundance of herons during the winter along the Gulf of Mexico Coast (Mikuska *et al.* 1998). Better knowledge of important wintering habitat can assist the conservation of wading birds. Winter condition has been shown to be important to herons in other parts of the world. For example, severe winter weather has been shown to adversely affect the population stability of Grey Herons (*Ardea cinerea*) in Great Britain (North and Morgan 1979), and Purple Heron (*Ardea purpurea)* populations are affected by conditions at wintering sites in West Africa (den Held 1981; Cave 1983). These studies indicated that severe weather events constrained resource acquisition by wading birds and subsequently affect population stability.

Sympatric wading birds partition resources using a variety of factors including habitat (Kushlan 1978; Frederick and Bildstein 1992; Ramo and Busto 1993; Chavez-Ramirez and Slack 1995), food resources (Kushlan 1981; Maccarone and Parsons 1994) and behavior (Willard 1977; Kent 1986). Generally during the breeding season, resources appear to be divided with a high degree of overlap among species of similar sizes (Jenni 1969; Willard 1977; Custer and Osborn 1978a; Kent 1986) and low degree of overlap among herons of different sizes (Willard 1977). In contrast, Chavez-Ramirez and Slack (1995) found that species that were most similar in size showed the least overlap in patterns of habitat use. They argued that this could reflect differences between breeding and non-breeding seasons, and that factors including changes in prey availability, similar use of food resources among similarly sized species and habitat selection where preferred food may be found could have altered patterns of habitat use during the non-breeding season (Chavez-Ramirez and Slack 1995).

The purpose of this study was to determine landscape level patterns of habitat use by wintering wading birds in three different regions of the Gulf of Mexico coast. Specifically, I report on the patterns of landscape habitat types used among several species of wading birds on coastal marshes in Louisiana and Florida during the winter of 1997-98. I also compare data from Louisiana and Florida with similar data from Texas during the winter of 1996-97.

METHODS

Study Areas

I studied wading bird use of coastal salt marsh habitats types at three different regions of

the Gulf of Mexico coast. The first region was represented by Aransas National Wildlife Refuge (ANWR), located in the coastal bend region of Texas, Calhoun County (Fig. 3.1). The salt marsh areas were located on the eastern coast of the refuge and consisted of vegetated flats dominated by glasswort, saltwort, sea-oxeye daisy, wolfberry, saltgrass, smooth cordgrass, and wind tidal flats dominated by mudflat grass, saltgrass and cordgrasses. Interspersed among vegetated areas are bodies of open-water of varying sizes (Chavez-Ramirez and Slack 1995).

The second region was represented by Marsh Island and Wildlife Refuge and Game Preserve (MIWR), located off the southern coast of Louisiana between Vermillion Bay and the Gulf of Mexico (Fig 3.2). Prominent marsh vegetation includes wire grass (*Spartina patens*), three corner grass (*Scirpus americanus*), and black needle rush (*Juncus roemerianus*). Shrub species such as salt bush (*Baccaris halimifolia*) and marsh elder (*Iva frutescens*) occur along spoil banks. There are also several tree species including: hackberry (*Celtis laevigata*), Chinese tallow (*Sapium sebiferum*), chinaberry (*Melia asedrarach*), Toothache tree (*Zanthoxylum clava-herculis*) and Huisache (*Acacia farnesiana*).

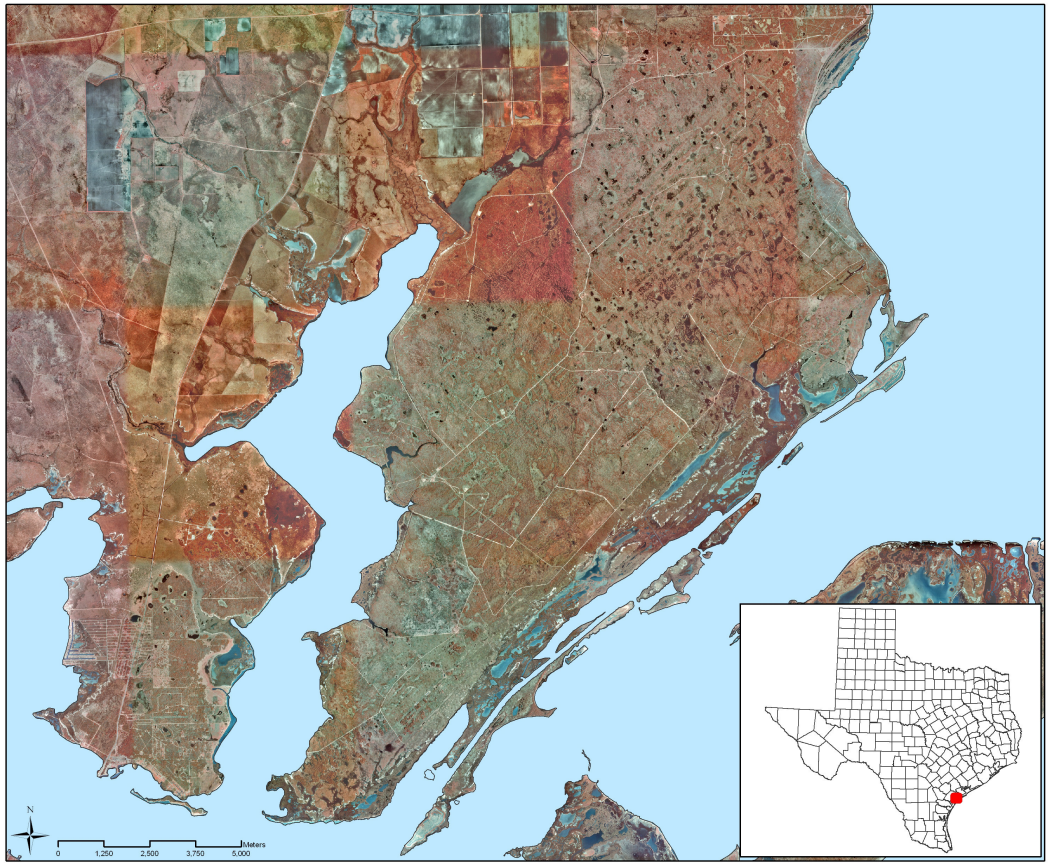

Figure 3. 1. Map of ANWR, Texas.

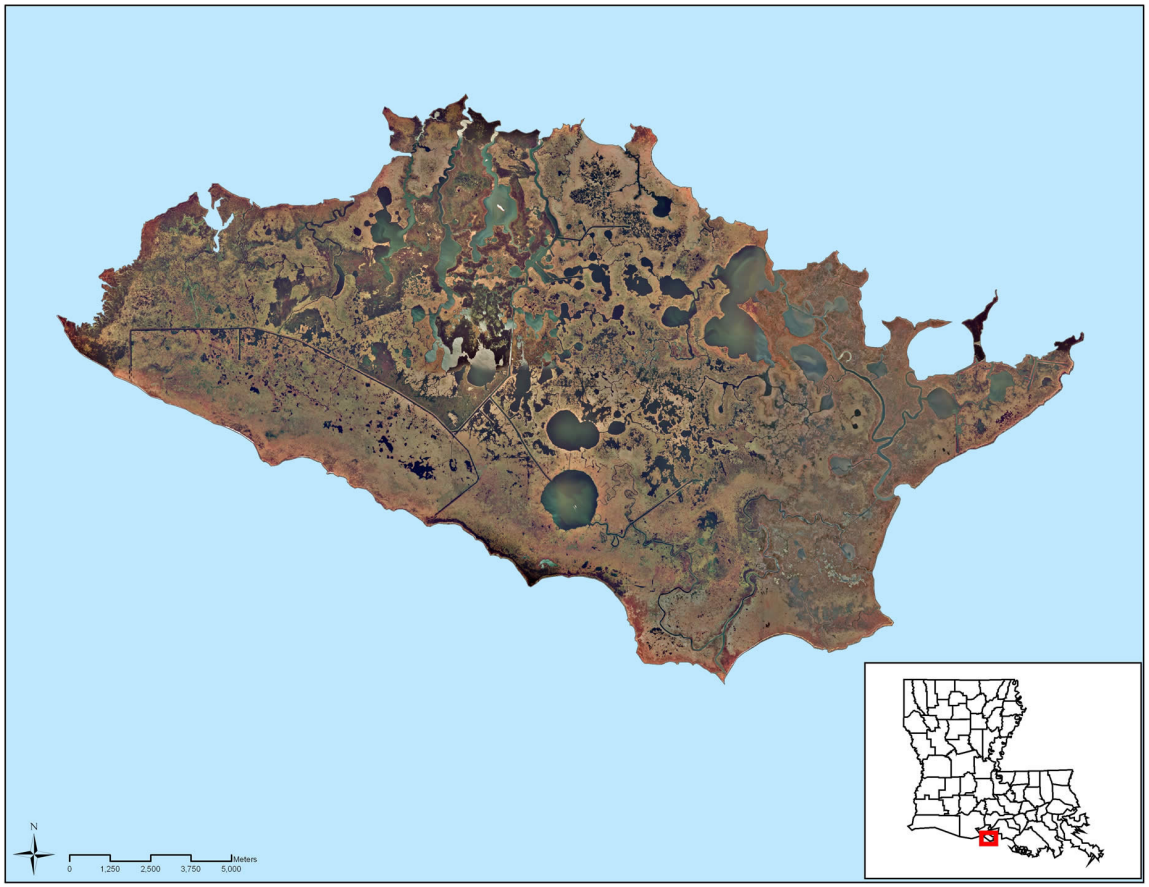

Figure 3. 2. Map of MIWR, Louisiana.

The region in Florida was represented by a study site encompassing two adjacent areas (Fig. 3.3), the St. Martin's Marsh Aquatic Preserve (SMMAP), which was located in Citrus County and the Chassahowitzka NWR (CNWR), which was located in both Citrus and Hernando counties. CNWR and the adjacent Preserve are composed of open water, inlet bays, tidal rivers and creeks, and salt marsh. The major plant community associations found here include salt marsh, tidal flats, marine grassbeds, mangrove forest and hammock islands. The majority of research was conducted in salt marsh areas. The dominant plant species here are black needle rush, salt grass and smooth cordgrass. Additionally, there are many areas of marine grassbeds, vegetated by such grasses as turtle grass and shoalgrass. The water in these areas was known for its high clarity (St. Martins Marsh Aquatic Preserve Management Plan. Department of Natural Resources. September 9, 1987).

Flights

At ANWR observations of wading bird habitat use were made from a fixed-wing aircraft from 12 December 1996 through 31 December 1996. A total of 3 flights were conducted on December 12, 18 and 31. During each flight, transects were flown parallel to the coastline at an

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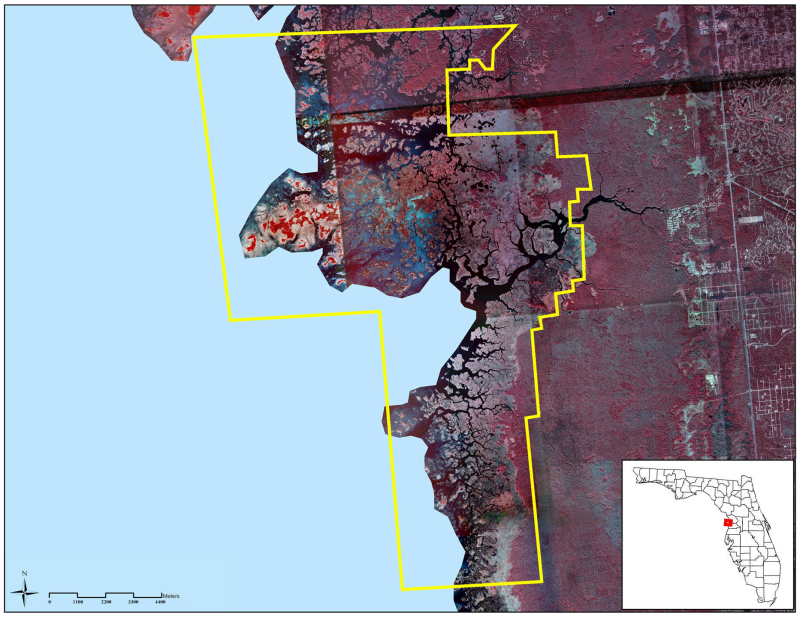

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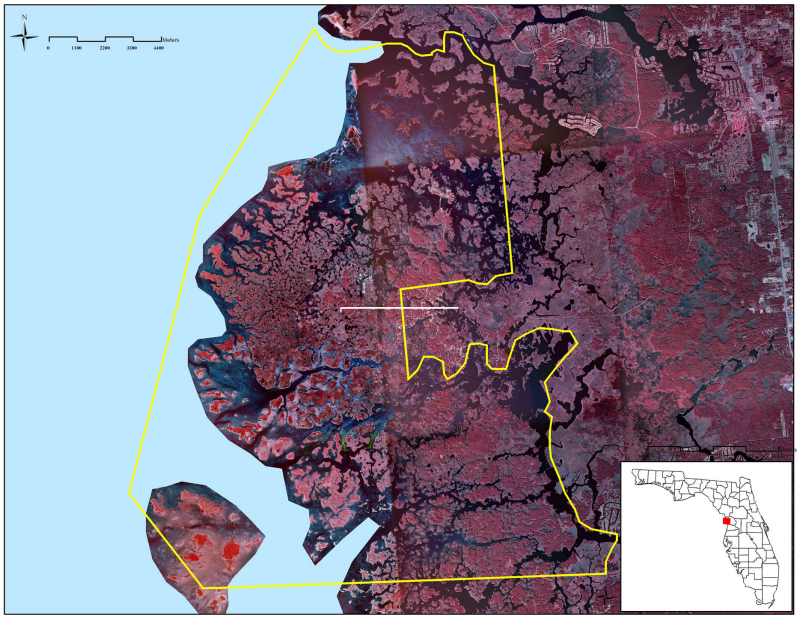

Figure 3.3 Maps of A) CNWR and B) St. Martin's Marsh Aquatic Preserve (SMMAP), Florida.

altitude between 30 and 50 m. A linear distance of approximately 175 km was covered on each flight. The first transect was flown along the coast with successive transects approximately 0.5 km inland from the previous one. Due to the large proportion of wading birds present in the marshes, only wading birds observed within 25 m perpendicular to the flight line on the observer's side of the aircraft were identified and habitat type in which each was located was recorded. Birds not identified to species were eliminated from the analysis. Individual observations where habitats could not be confidently classified (e.g., pond vs. pool) were not used in the analysis.

Flights conducted on a fixed-wing aircraft were used to locate wading birds and define habitat types on which they were present. Aerial flights were not used to measure abundance or density of birds in different regions. I conducted two flights over MIWR, Louisiana and three flights over CNWR/SMMAP, Florida to determine distribution and abundance of wading birds. Inclement weather events prevented more aerial surveys at these sites. Each survey of MIWR consisted of fourteen flight lines, approximately 1.6 km apart (east to west), flown in a north to south direction for a total linear distance of 135 km flown during each survey. Transects in MIWR were conducted on 5 December 1997 and 13 February 1998, respectively. Five flight lines approximately 1.62 km apart (east to west) were flown over CNWR/ SMMAP from north to south, for a total linear distance flown of 60 km per survey. Flights were conducted in Florida during 21 January, 20 February, and 1 April, 1998, respectively. Flights to observe wading birds were generally conducted between 30.5 and 61 m in order to locate and identify species more easily. Due to flying restrictions in Florida, surveys could not be conducted below 152.4 m, which made locating and differentiating Tricolored and Little Blue Herons difficult; therefore neither species was tallied at this site.

Flights were focused on locating the following species of wading birds: Great Blue Herons, Great Egrets, Snowy Egrets, Little Blue Herons, Reddish Egrets, Tricolored Herons, Roseate Spoonbills and White Ibises, (with the exception of Tricolored and Little Blue Herons in Florida aerial surveys). Within all three regions the landscapes flown had similar landscape elements consisting of open water and vegetated patches of variable sizes. In order to determine the dispersion of flocks and individuals throughout the landscape, I classified open-water habitats into five types based on the aerial extent as follows: ponds (0-100 m^2), lakes (>100 m^2), bays (shallow open-water area adjacent to coast), cuts (narrow straight or winding, open-water areas connecting two or more bodies of water except bays) and inlets (same as cuts only connected on one end to a bay) (Chavez-Ramirez and Slack 1995). Vegetated flat was the only non-open water category. I recorded individual birds, and species proportions within flocks, separately within each category.

Statistics

I compared patterns of habitat use by all wading birds among regions using a Chi-square test (Conover 1999). Two species, Great Egrets and Great Blue herons were observed at all three locations. I used a chi-square goodness of fit test to test the hypothesis that Great Egrets and Great Blue Herons had similar habitat use at all locations (Conover 1999). There is currently little data on foraging wading bird habitat use patterns for the nonbreeding season. Therefore I assumed that all habitat types defined were equally likely to be used by a species. I compared patterns of habitat use by all wading bird species within a region using a chi-square test. To determine if species within a region used all habitat categories equally, I used chi-square goodness of fit tests.

Within each region, I calculated niche overlap using Pianka's niche overlap index for each pair of species:

$$O_{12} = O_{21} = \frac{\sum_{i=1}^{n} (p_{2i})(p_{1i})}{\sqrt{\sum_{i=1}^{n} (p_{2i})^2 (p_{1i})^2}}$$

Where p_{1i} and p_{2i} represent the proportions of the *i*th resource used by the 1st and 2nd species respectively. And the overlap of species one on species two (O_{12}) and overlap of species two on one (O_{21}) are symmetric or equal. This equation can generate values between zero or one with the higher the niche overlap the closer the index is to one (Pianka 1973). Dendrograms were built (average method) using the overlap indexes between species.

RESULTS

Comparisons Among Regions

Wading bird communities varied in species composition among regions. The most species rich wading bird assemblage was observed in Texas, with eight species located on aerial surveys. Species observed in Texas included Great Egrets (N =1091), Snowy Egrets (N = 460), Tricolored Herons (N = 50), Reddish Egrets (N = 75), Roseate Spoonbills (N = 433), White Ibis (N = 856) and Great Blue Herons (N = 133). Little Blue Herons (N = 5) were dropped from analyses because of small sample sizes for a total of (N = 3098) birds.

In Louisiana, six wading bird species were observed during wading bird flights: Great Egrets (N = 101), Snowy Egrets (N = 112), Tricolored Herons (N = 5), Roseate Spoonbills (N = 110), Great Blue Herons (N = 45) and one Little Blue Heron. Tricolored Herons (N = 5) and Little Blue Herons (N = 1) were dropped from the analyses because of small sample sizes for a total of (N = 368) birds. Florida had the lowest recorded richness for the wading bird assemblage with only 3 species consistently observed on flights. Species observed in Florida included Great Egrets (N = 338), White Ibis (N = 17) and Great Blue Herons (N = 29) for a total of (N = 384).

Patterns of wintering wading bird habitat use were significantly different among regions (χ^2 = 2623.9, p < .001) (Fig. 3.4). At ANWR, wading birds were observed most often in ponds, vegetated areas and lakes. Wading birds rarely utilized bays, cuts or inlets. At MIWR, wading birds were observed most often in pools, cuts, lakes and ponds. They were observed using bays, inlets and vegetated areas to a much lesser extent. At CNWR, wading bird patterns of habitat use were different compared to the other locations with the birds observed most frequently using inlets and bays. They were observed much less often in lakes, ponds, vegetated areas and cuts and they were never observed in pools.

Only two species were observed at all sites, Great Egrets and Great Blue Herons. When I compared the habitat use of these species among regions, I found that habitat use varied significantly among regions for each species. Great Egrets at ANWR were observed more often than expected in vegetated areas (χ^2 = 1206.5, *df* = 6) (Fig 3.5). Great Egrets and Great Blue Herons were observed as expected or less than expected in all other habitats. At MIWR, Great Egrets were observed more often than expected in ponds, lakes and cuts (χ^2 = 120.2, *df* = 6). Great Egrets and Great Blue Herons were not observed in pools and were observed less often than expected in bays, inlets and vegetated areas. At CNWR Great Egrets were observed most often in inlets and bays (χ^2 = 620.3, *df* = 6). They were observed less often than expected in cuts, lakes and ponds and they were not observed at all in pools.

Great Blue Herons at ANWR were observed more often than expected in vegetated flats and to a lesser extent in lakes (Fig. 3.6). At MIWR, they were also observed more often than expected in lakes, and in cuts and ponds as well. At CNWR they were observed more often than expected in bays, inlets and ponds.

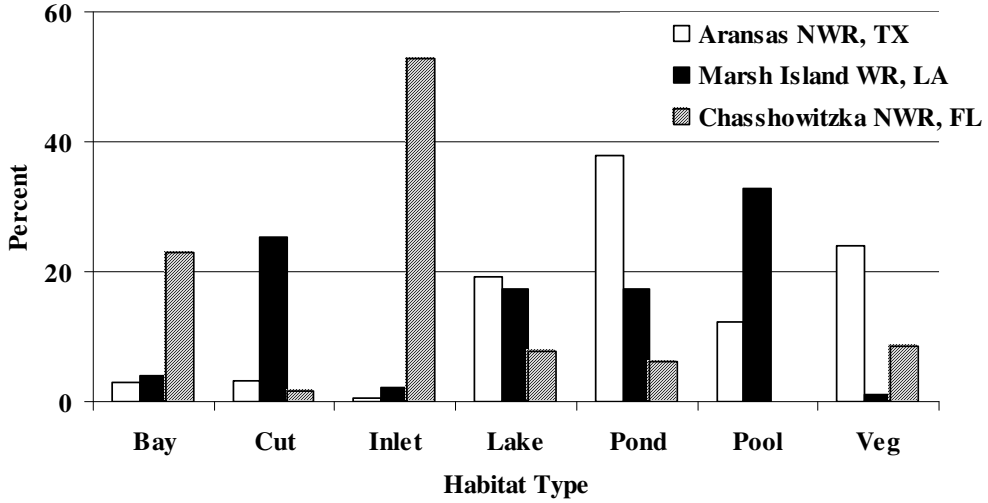

Figure 3.4. Habitat type use patterns of all wading bird species combined, compared among ANWR, Texas, MIWR, Louisiana and CNWR, FL during the winter season of 1997-1998.

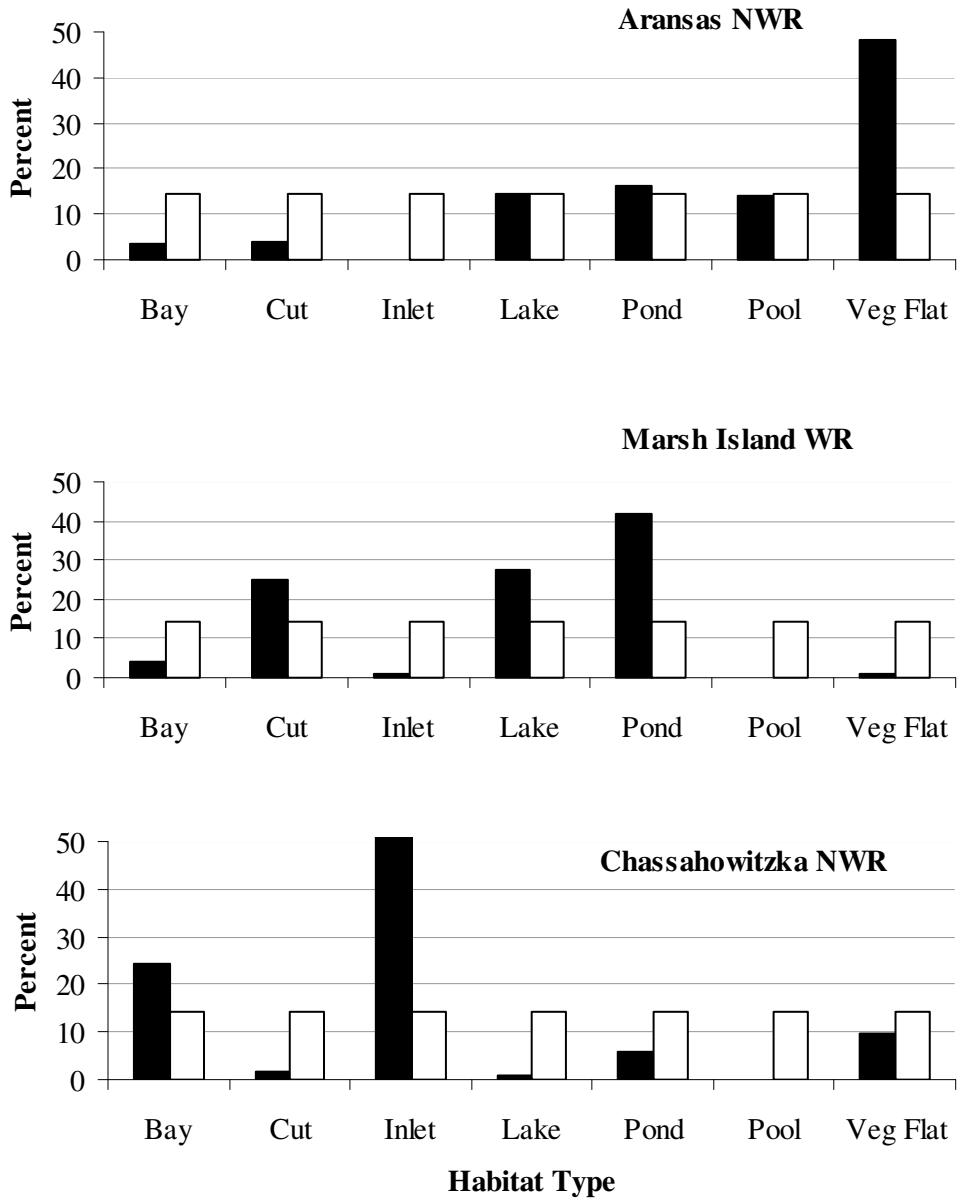

Figure 3.5. Patterns of wintering habitat use by Great Egrets at ANWR, MIWR and CNWR for the winter seasons of 1997-98. White bars represent proportion of individuals expected and black bars indicate proportion of individuals observed.

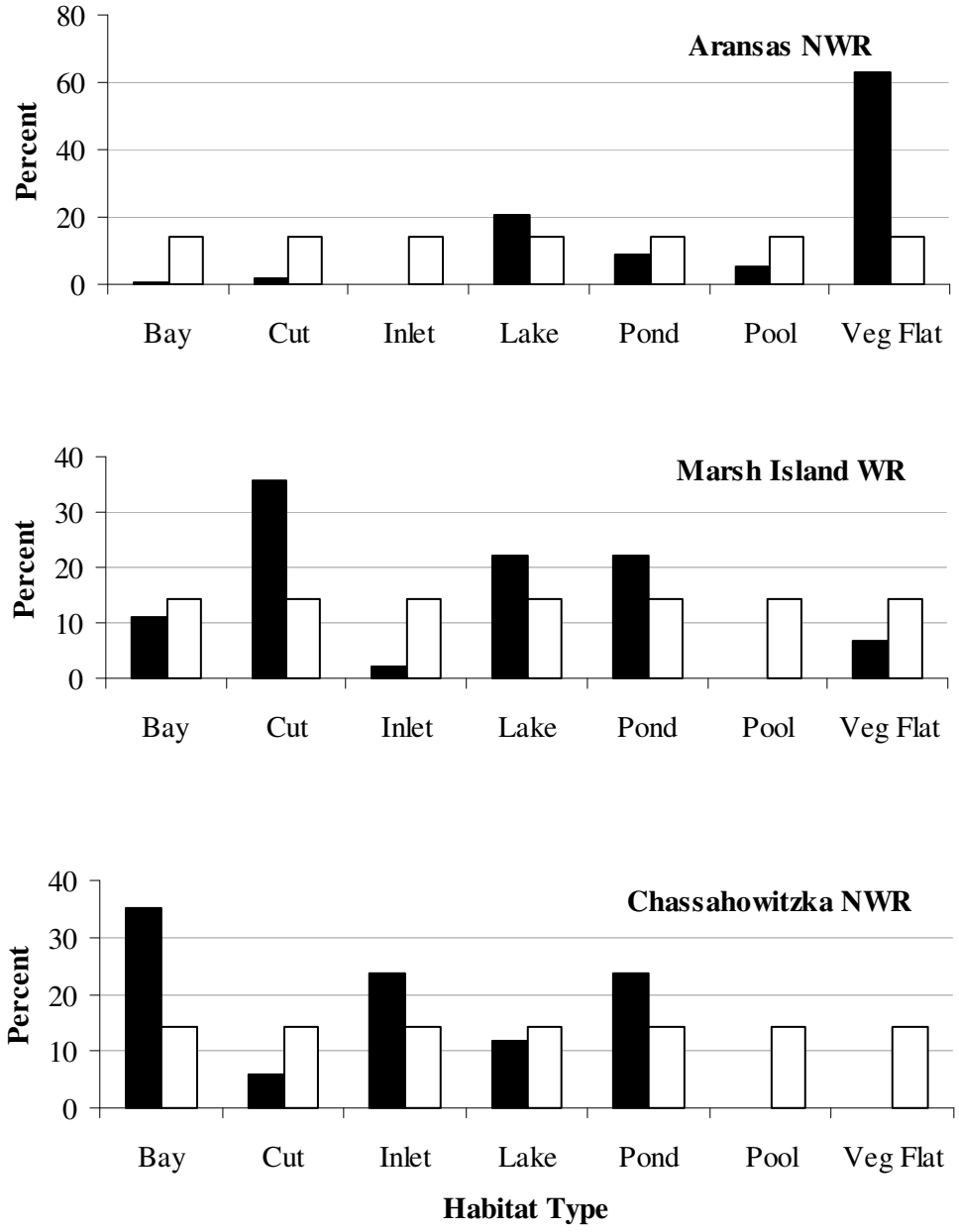

Figure 3.6. Patterns of wintering habitat use by Great Blue Herons at ANWR, MIWR and CNWR for the winter seasons of 1997-98. White bars represent proportion of individuals expected and black bars indicate proportion of individuals observed.

Comparisons Within Region

Patterns of wading bird habitat use were significantly different among species within each region. At ANWR habitat use varied among species (χ^2=1557.2, *df* = 36, *p* <.001). All species used ponds, lakes and vegetated areas more often than expected (Fig. 3.7). Great Egrets used vegetated flats more often than expected and all other areas as expected or less than expected (Fig. 3.8A). Ponds, lakes, vegetated flats and pools were all used more often than expected by Snowy Egrets (Fig. 3.8B). Tricolored Herons used lakes and pools more often than expected (Fig. 3.9A). They used all other habitat categories less than expected and were not observed in either cuts or inlets. Reddish Egrets used lakes, ponds and pools more often than expected, however they were never observed in vegetated flats, cuts or inlets (Fig. 3.9B). Roseate Spoonbills were observed more often than expected in lakes and pools (Fig. 3.10A), whereas White Ibis were observed more often than expected only in ponds (Fig. 3.10B). They were observed less often than expected in lakes, pools and bays and they were not observed in vegetated areas, inlets or cuts. Great Blue Herons were observed more often than expected in vegetated areas and lakes, and less often than expected in pools, ponds, bays and cuts (Fig. 3.11). They were not observed in inlets.

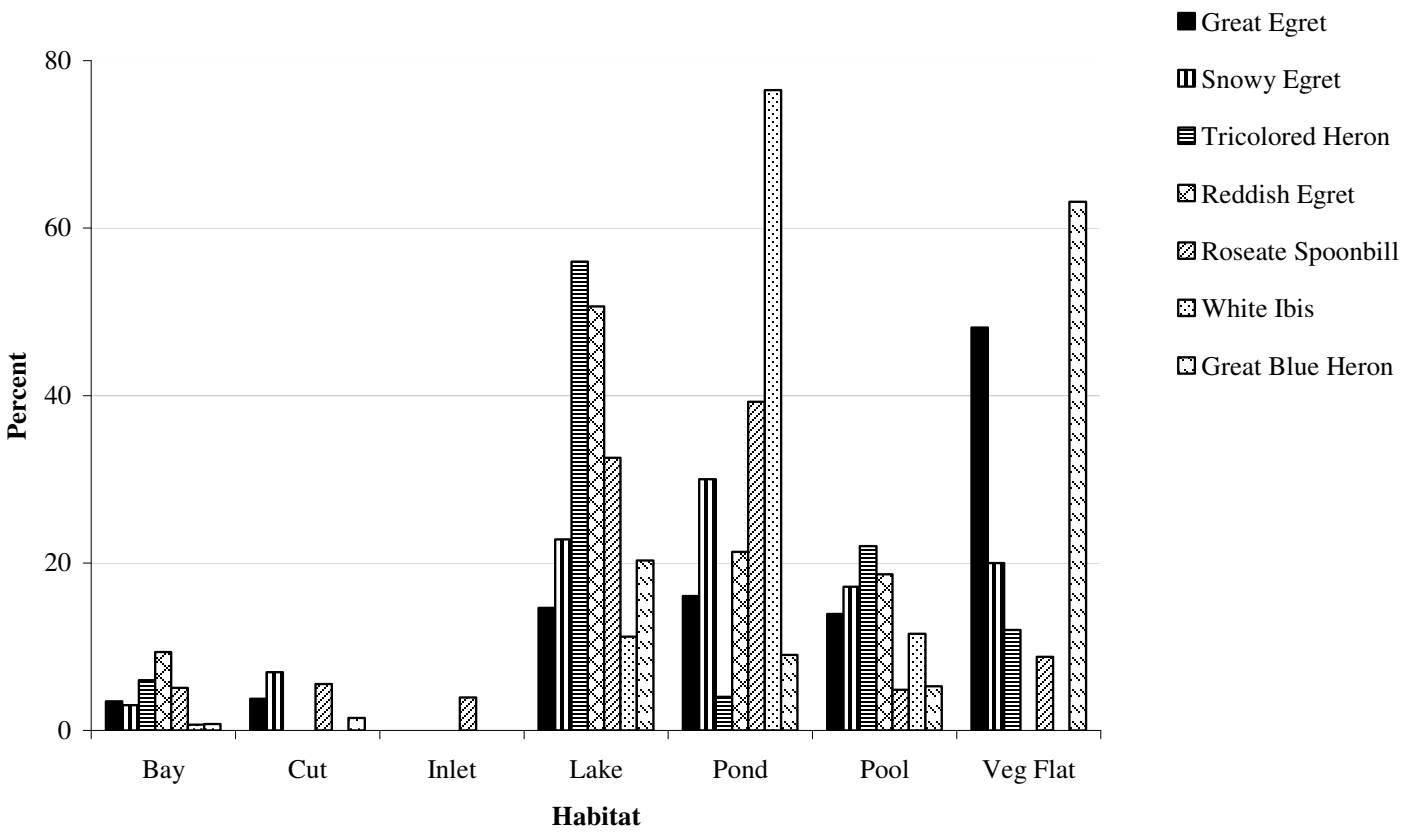

Figure 3.7. Patterns of wintering wading bird habitat use at ANWR in December 1996.

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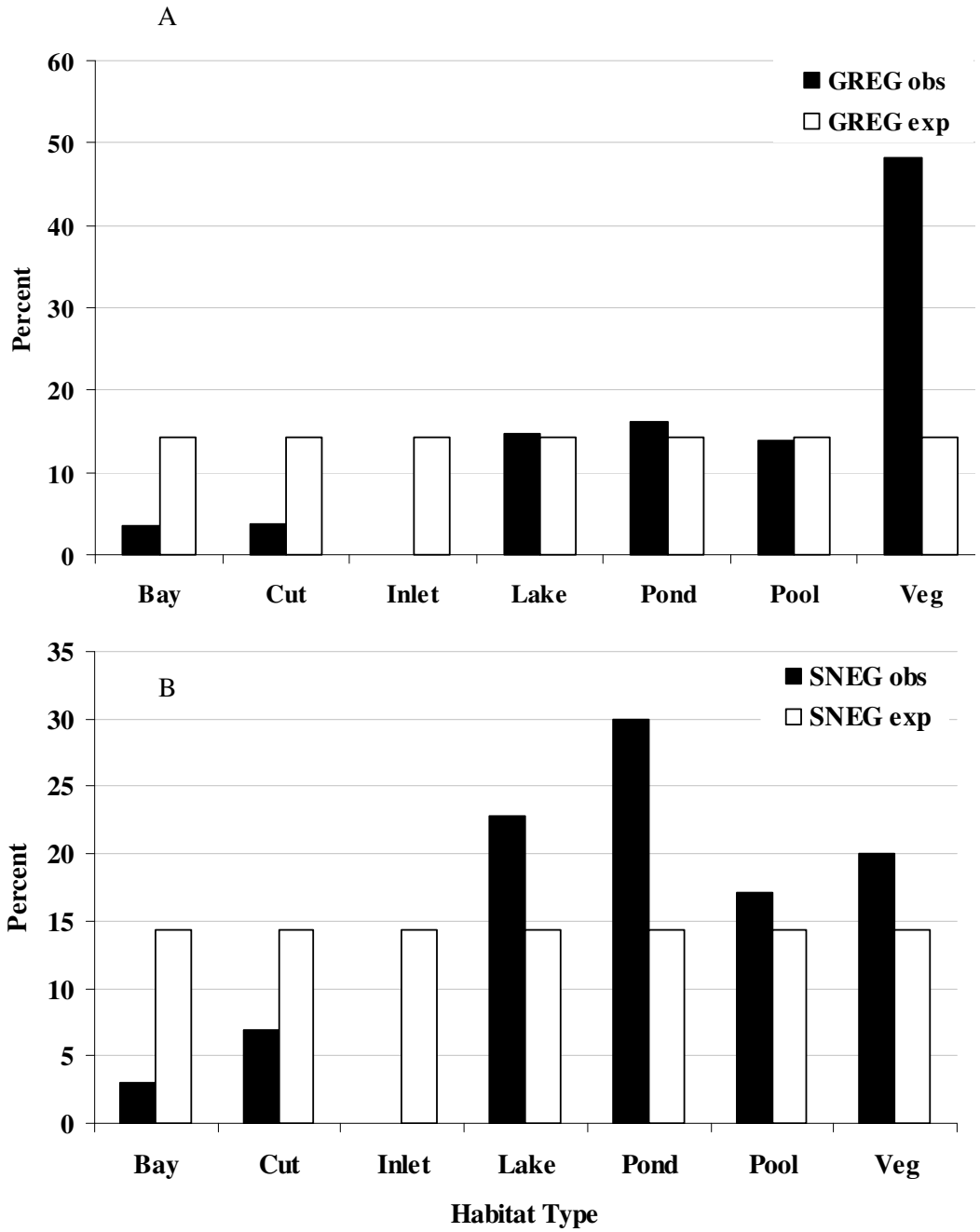

Figure 3.8. A) Patterns of habitat use by Great Egrets and B) Snowy Egrets at ANWR, TX in December 1996. White bars represent proportion of individuals expected and black bars indicate proportion of individuals observed.

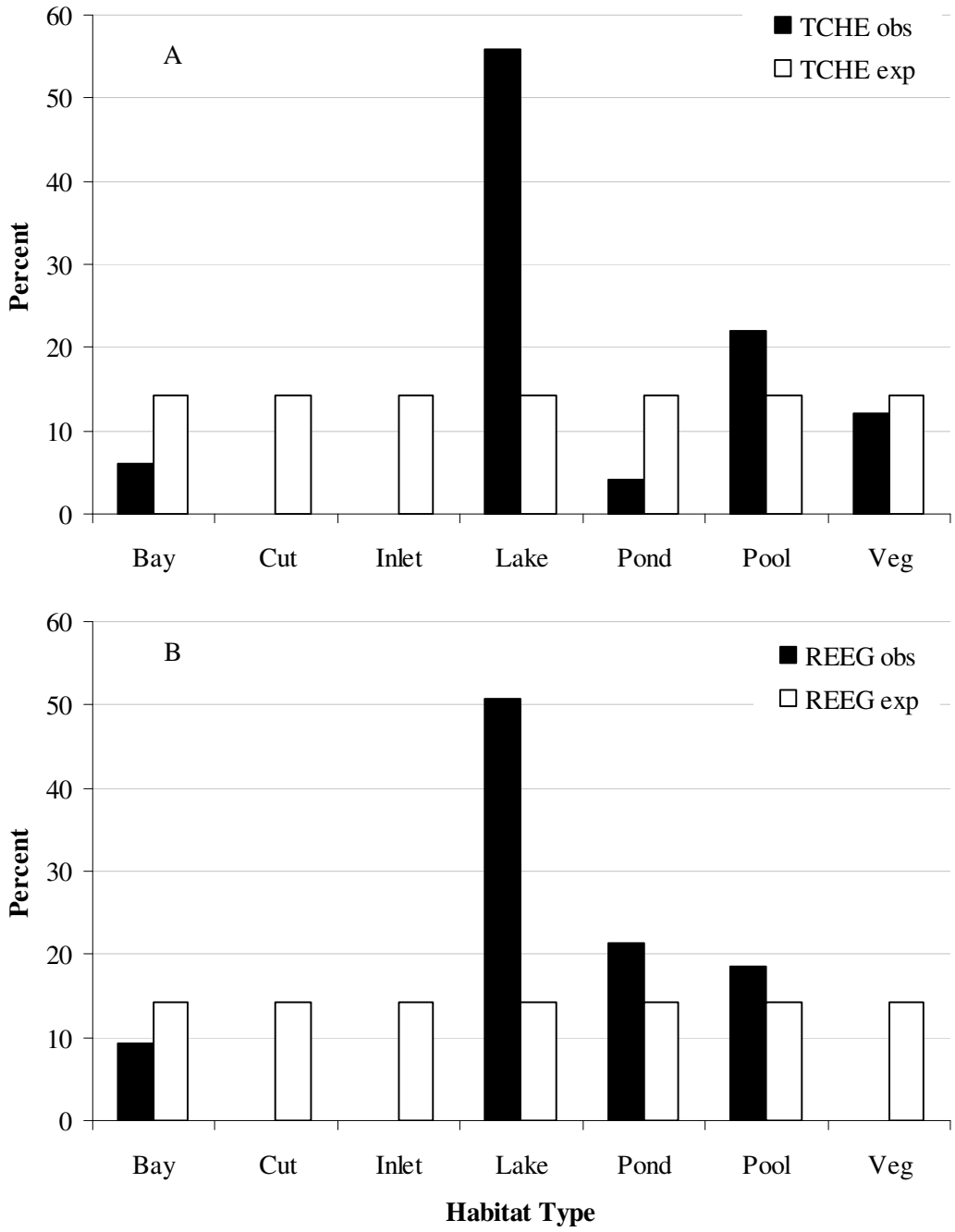

Figure 3.9. A) Patterns of habitat use by Tricolored Herons and B) Reddish Egrets at ANWR, TX in December 1996. White bars represent proportion of individuals expected and black bars indicate proportion of individuals observed.
Figure 3.10. A) Patterns of habitat use by Roseate Spoonbills and B) White Ibis at ANWR, TX in December 1996. White bars represent proportion of individuals expected and black bars indicate proportion of individuals observed.

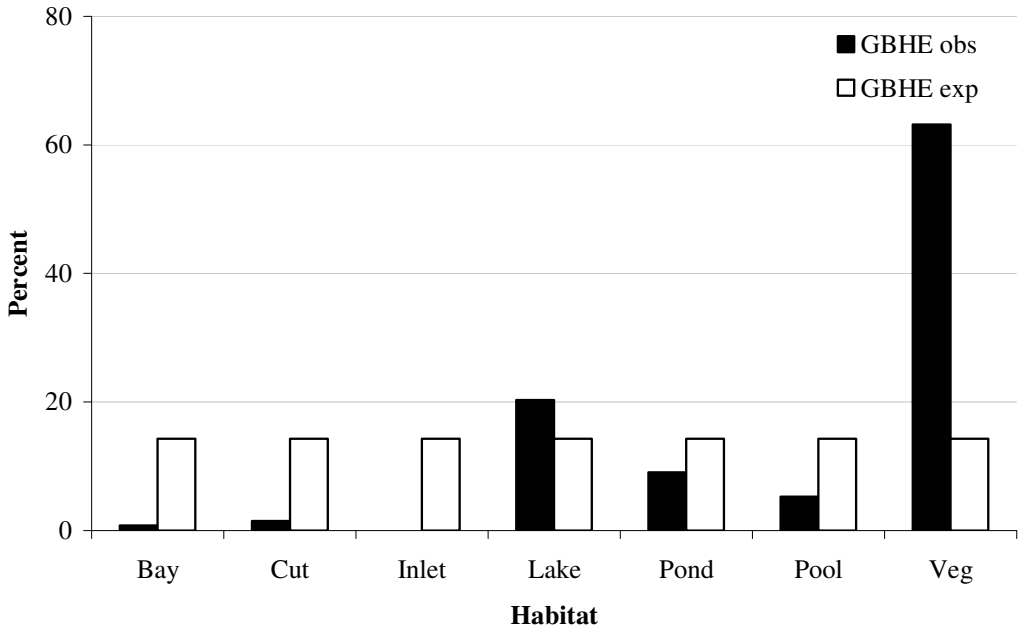

Figure 3.11. Patterns of habitat use by Great Blue Herons at ANWR, TX in December 1996. White bars represent proportion of individuals expected and black bars indicate proportion of individuals observed.

.

Habitat use was significantly different among wading bird species at MIWR (χ^2 = 99.3, *df* = 18) (Fig. 3.12). All species used cuts, bays and ponds more often than expected, whereas lakes, inlets and vegetated areas were used less often than expected. Great Egrets were observed in ponds, lakes and cuts more often than expected (Fig. 3.13A) and in bays, inlets and vegetated areas less often than expected. Snowy Egrets only used the ponds more often than expected (Fig. 3.13B). All other habitats were used either as expected or less often than expected. Roseate Spoonbills were observed in ponds and cuts more often than expected and less often than expected in lakes and inlets (Fig. 3.14A). They were not observed in bays or vegetated areas. Great Blue Herons used cuts, lakes and ponds more often than expected and all other habitats less often than expected (Fig. 3.14B).

Although only three species were observed at the Florida sites, habitat use was also significantly different for each of these species (χ^2 = 286.9, *df* = 10) (Fig. 3.15). Goodness of fit tests indicated that Great Egrets used inlets and bays more often than expected, and vegetated areas, ponds, cuts and lakes less often than expected (Fig. 3.16A). Great Blue Herons used bays, inlets and ponds more often than expected and cuts and lakes less often then expected (Fig. 3.16B). Whereas White Ibis used lakes more often than expected, inlets less often then expected, and they were not observed in any other habitat (Fig. 3.17).

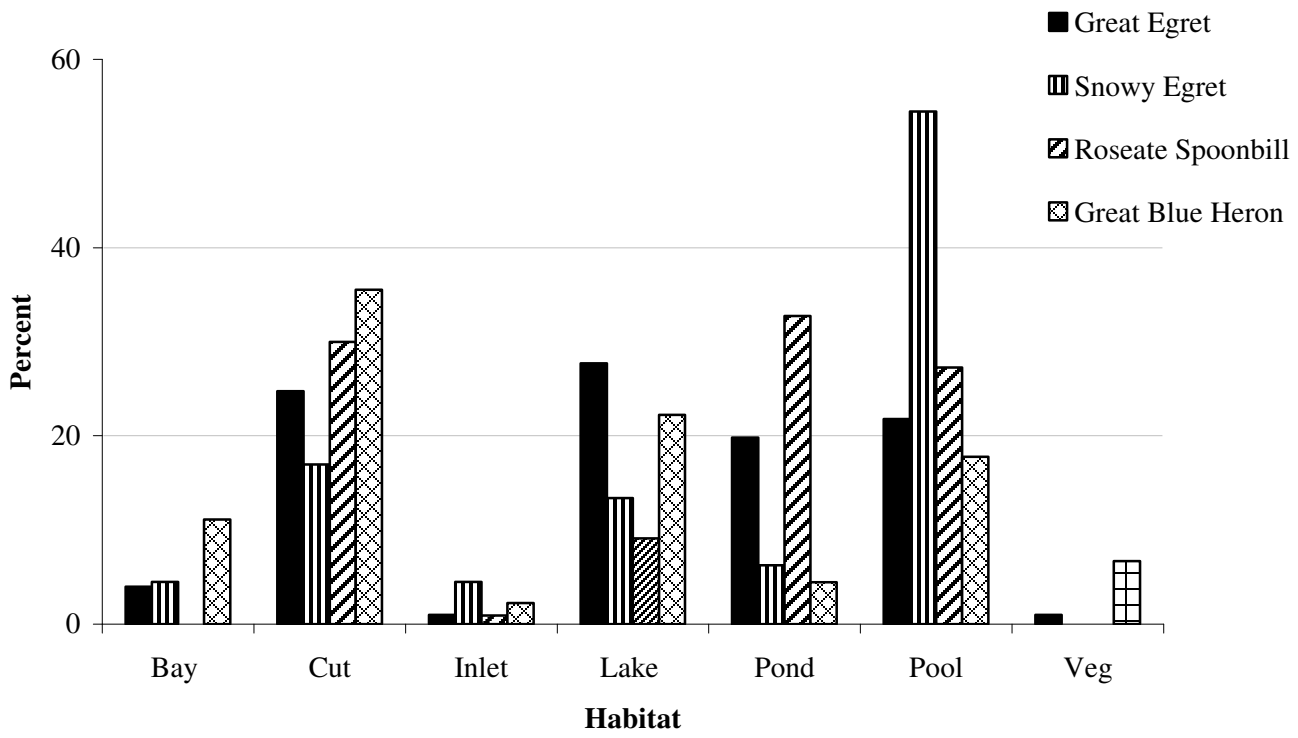

Figure 3.12. Patterns of wintering wading bird habitat use at MIWR, Louisiana during December 1997 and February 1998.

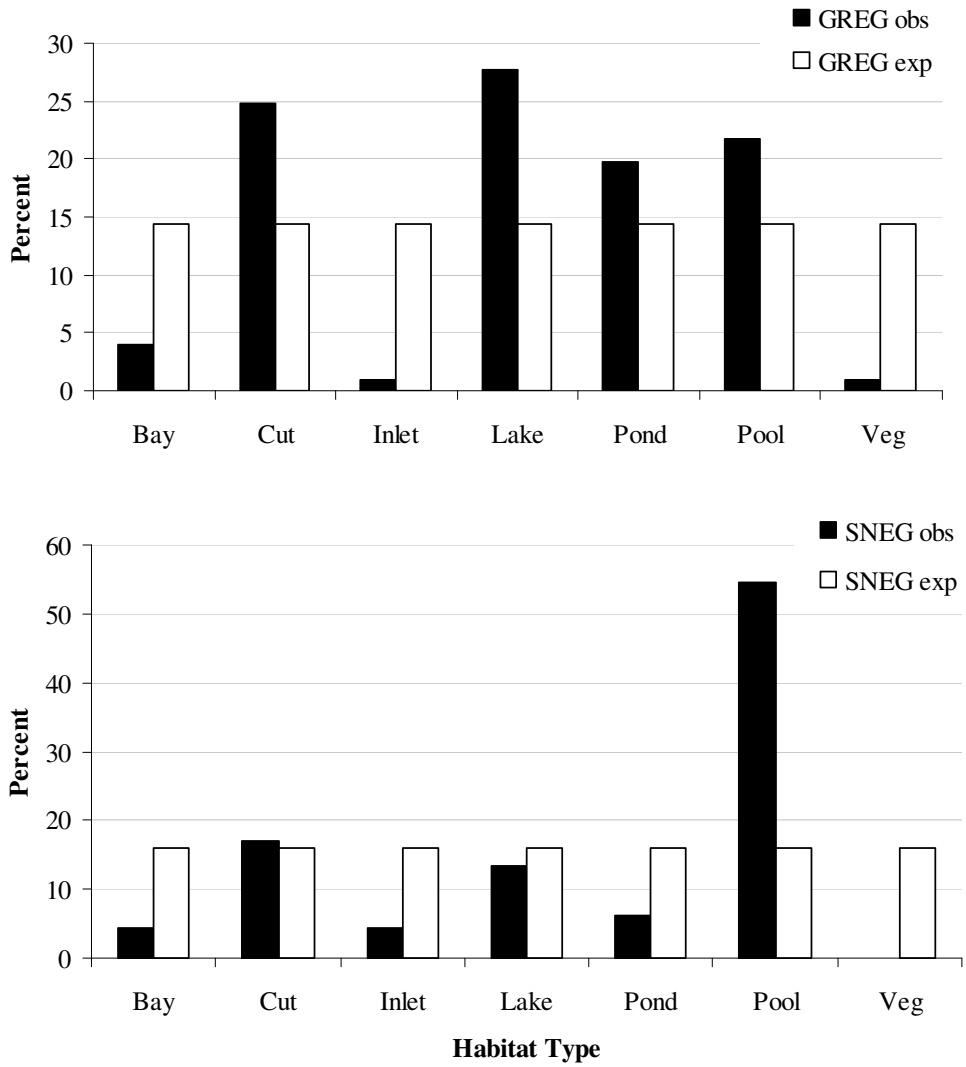

Figure 3.13. A) Patterns of habitat use by Great Egrets and B) Snowy Egrets at MIWR, LA during December 1997 and February 1998. White bars represent proportion of individuals expected and black bars indicate proportion of individuals observed.

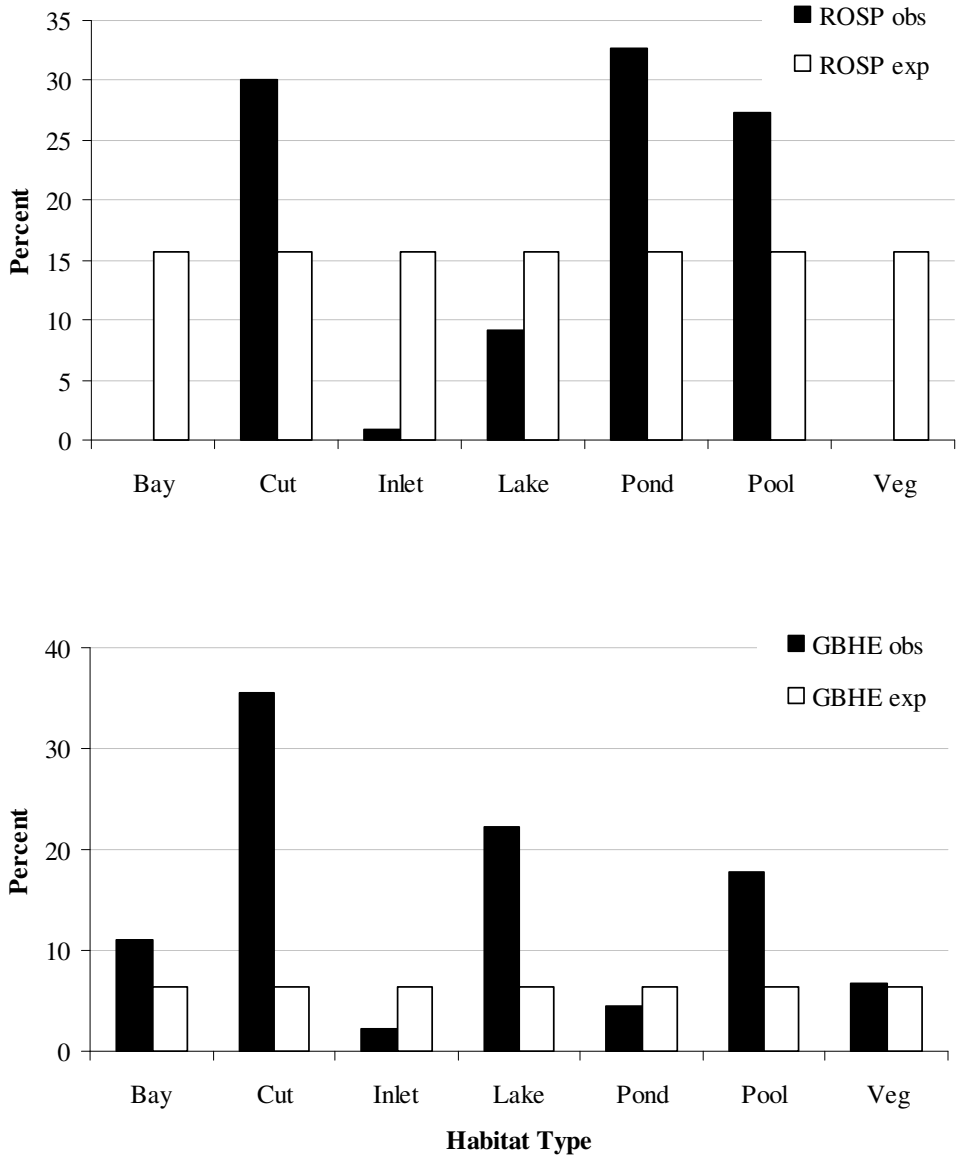

Figure 3.14. A) Patterns of habitat use by Roseate Spoonbills and B) Great Blue Herons at MIWR, LA during December 1997 and February 1998. White bars represent proportion of individuals expected and black bars indicate proportion of individuals observed

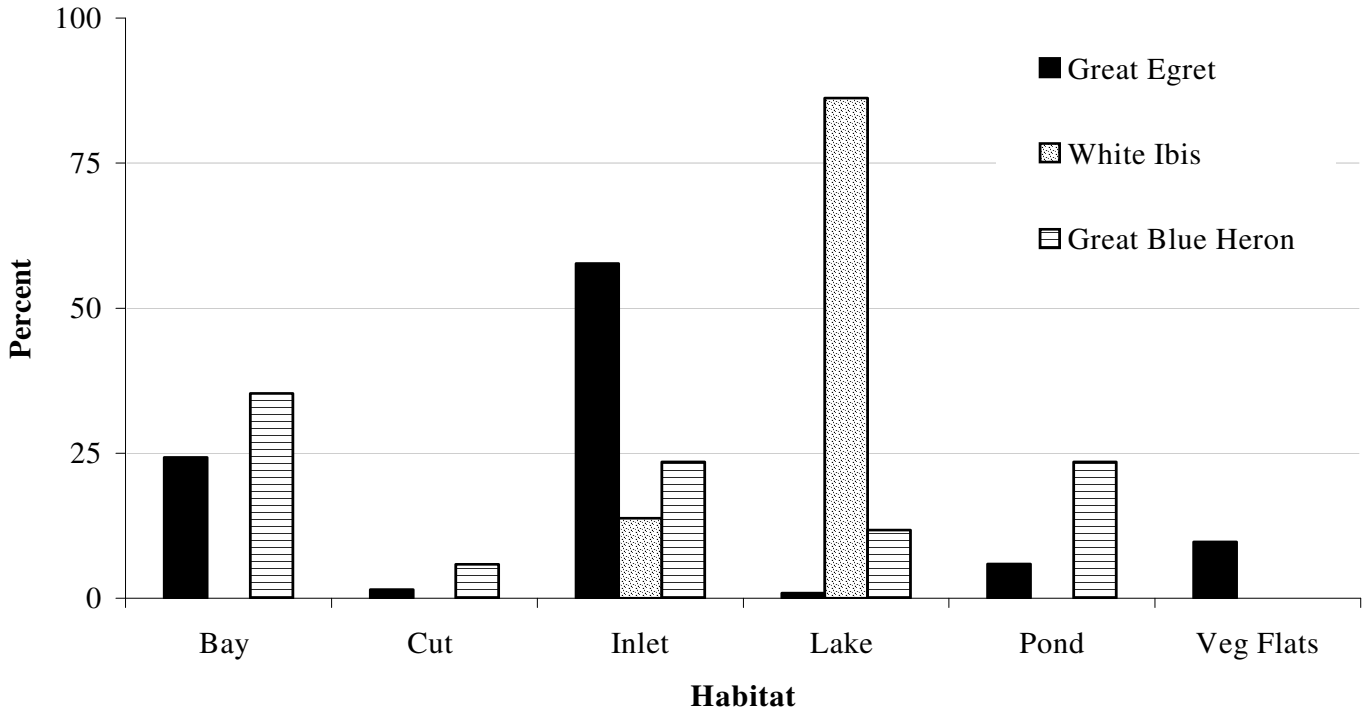

Figure 3.15. Patterns of wintering wading bird habitat use at CNWR, Florida during November 1997, February and March 1998.

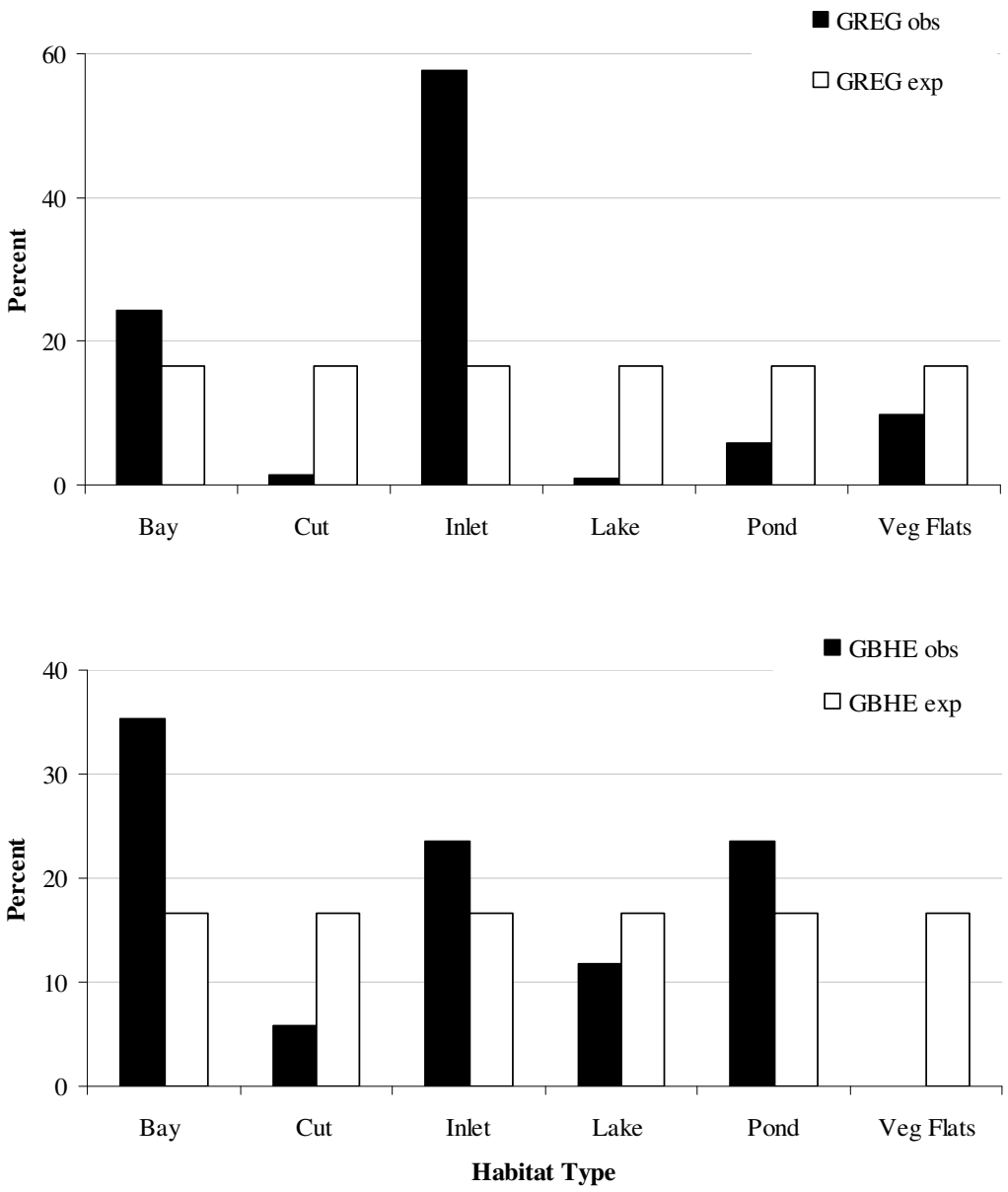

Figure 3.16. A) Patterns of habitat use by Great Egrets and B) Great Blue Herons at CNWR, FL during November 1997, February and March 1998. White bars represent proportion of individuals expected and black bars indicate proportion of individuals observed.

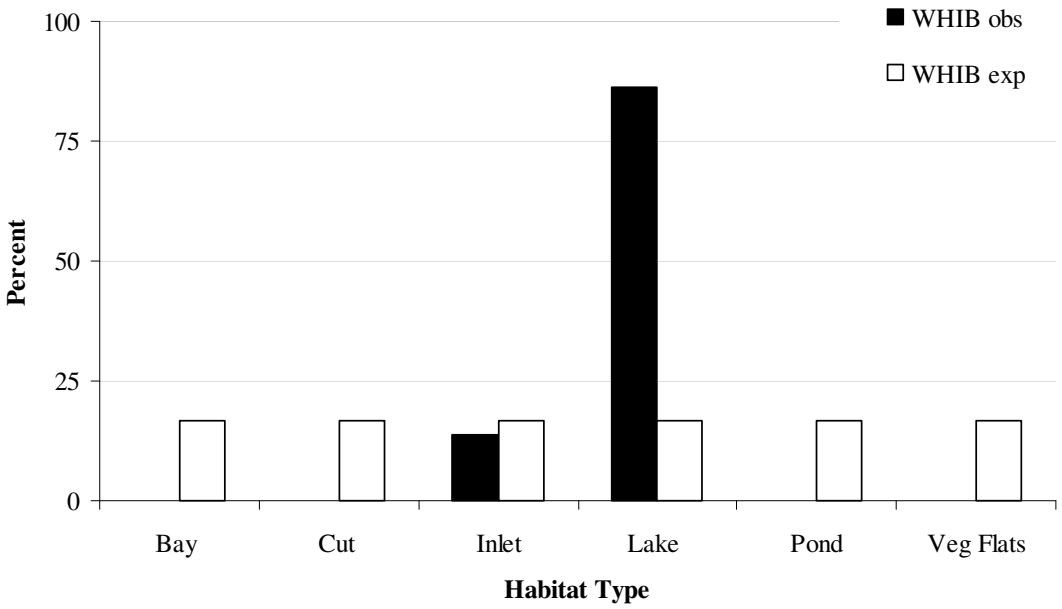

Figure 3.17. Patterns of habitat use by White Ibis at CNWR, FL during November 1997, February and March 1998. White bars represent proportion of individuals expected and black bars indicate proportion of individuals observed.

Overlap Indices

At ANWR, species of similar size had the highest calculated niche overlap (Fig. 3.18). For example, the two largest species, Great Egrets and Great Blue Herons, had the highest overlap in habitat use (0.97). Both of these species were observed most often in vegetated areas. Tricolored Herons and Reddish Egrets, both medium-sized species, had the next highest overlap in habitat use (0.93). These two species were observed more often than expected in lakes. This pattern, however, did not hold with the next species pair, Snowy Egrets and Roseate Spoonbills (0.91). Both of these species were observed most often in lakes and ponds. Snowy Egrets are among the smallest of the North American wading bird species (along with Little Blue Herons) whereas Roseate Spoonbills would fall into the medium-sized range. White Ibis had a much ower overlap index with the Roseate Spoonbill-Snowy Egret group (0.79). The White Ibis-Roseate Spoonbill-Snowy Egret complex overlapped in habitat use even less with the Reddish Egret-Tricolored Heron group (0.67).

And the lowest species overlap (0.53) occurred between the Great Egret-Great Blue Heron group and all other species. Great Egrets and Great Blue Herons also had the highest overlap in habitat use (0.89) at MIWR (Fig.3.19). Both of these species used cuts, lakes and pools more often than expected. Roseate Spoonbills had a slightly lower overlap in habitat use with Great Egrets and Great Blue Herons (0.82). Roseate Spoonbills, like Great Egrets and Great Blue Herons, used cuts and pools, but they were also observed in ponds more often than expected. Snowy Egrets showed the least overlap in habitat use (0.72) with other wading bird species. They were observed using only pools more often than expected.

Although only three species were observed, patterns of habitat overlap were similar at

CNWR (Fig. 3.20). Great Egrets and Great Blue Herons had the highest overlap in habitat use (0.74) although this was considerably less overlap than they showed in the other two locations. Both species used inlets and bays. Great Blue Herons also used ponds more often than expected and this probably accounted for the reduced overlap in habitat use. White Ibises overlapped the least (0.24) and were only observed in lakes more often than expected.

DISCUSSION

Patterns among Regions

Overall there was considerable variability in wintering wading bird habitat use among regions. Of the three regions, wading birds in Texas and Louisiana had the most similar patterns of habitat use, and birds were often observed in ponds, pools, lakes and vegetated flats. In Florida, wading birds used inlets and bays most often. Great Egrets and Great Blue Herons, the two species that occurred at all three locations, demonstrated these patterns of habitat use. In Texas, they were observed in vegetated flats, in Louisiana, they were observed using open water habitat that was not connected to a bay (e.g., ponds, lakes, cuts) and in Florida they were found mainly in inlets and bays.

One explanation for the variability in habitat use among regions was that wading birds selected habitats based on the prey available in those habitats. When geographic variability in use of foraging resources by wading birds in Europe was compared, each heron species was associated with a unique combination of habitat use and prey selection (Fasola 1994). Similarly, perhaps wading birds selected habitat in which prey was more readily captured. Whether inlets or cuts, both of these habitats have similar features in that they were narrow channels.

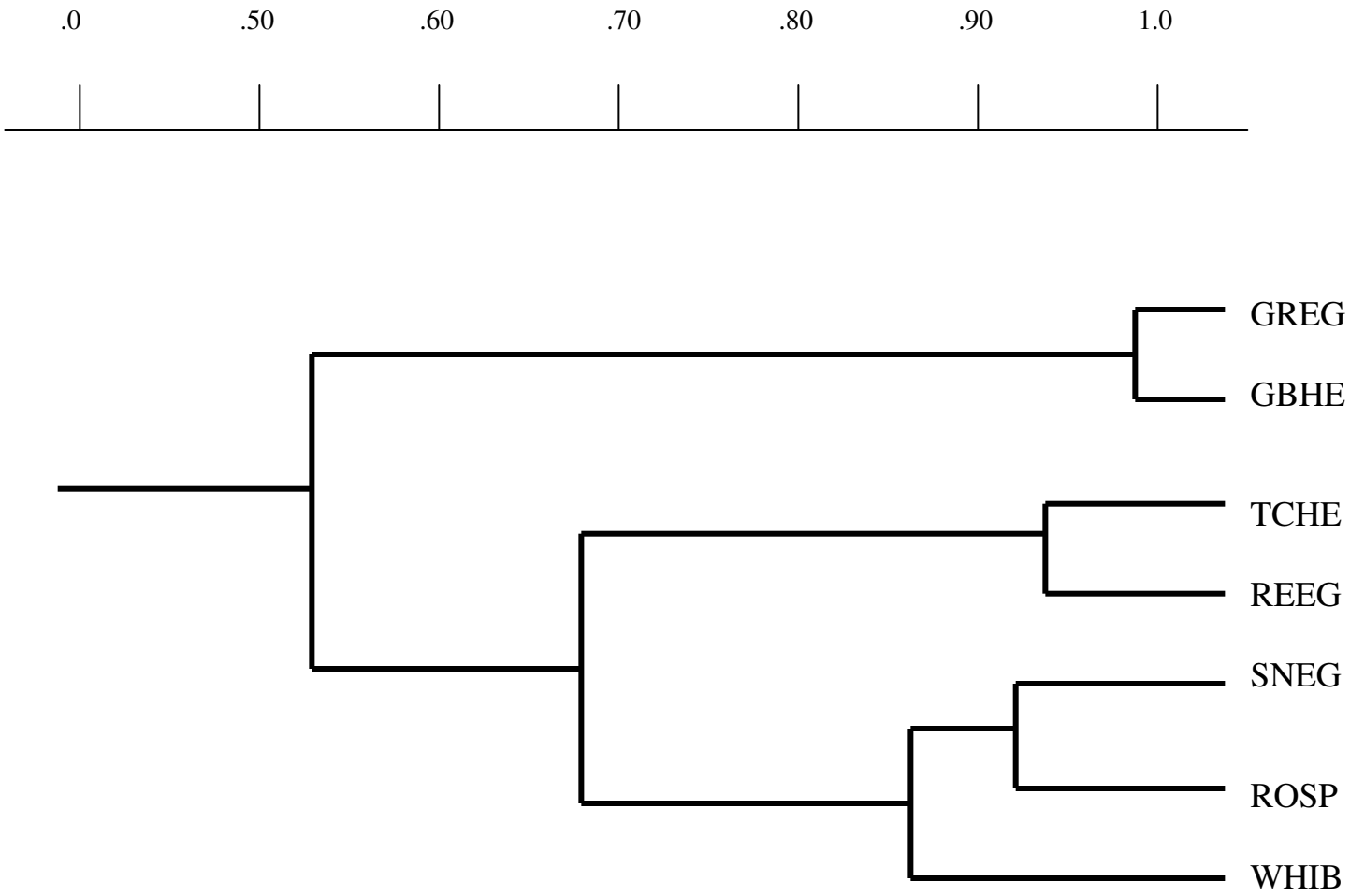

Figure 3.18. Dendrogram based on Pianka's niche overlap index calculated on habitat use patterns of all species pairs for ANWR, TX.

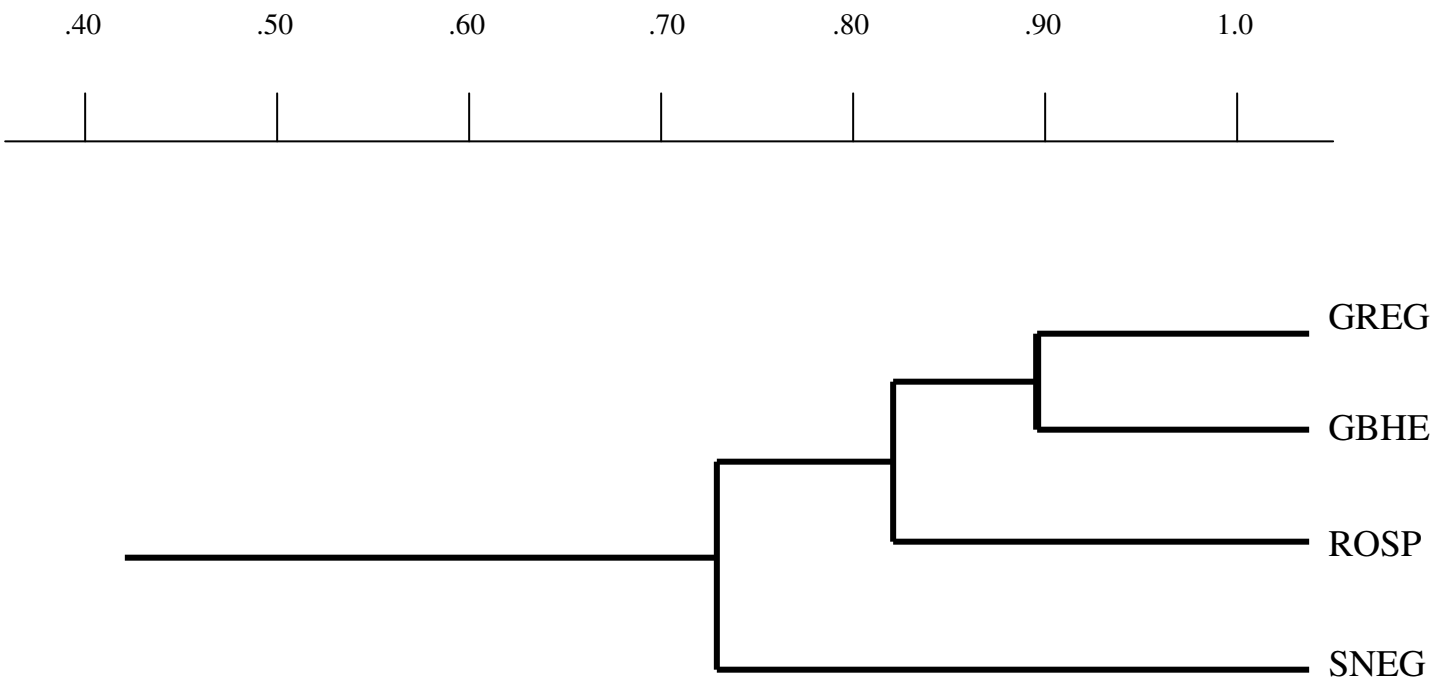

Figure 3.19. Dendrogram based on Pianka's niche overlap index calculated on habitat use patterns of all species pairs for MIWR, LA.

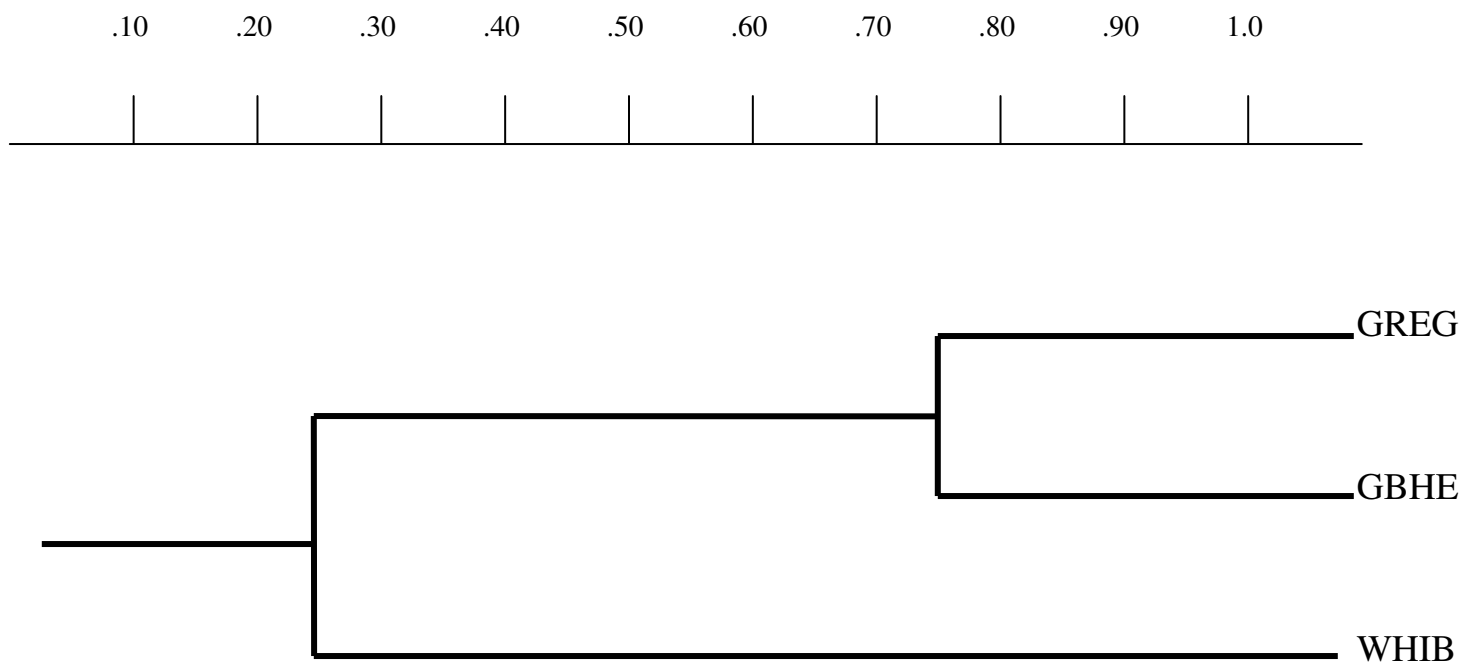

Figure 3.20. Dendrogram based on Pianka's niche overlap index calculated on habitat use patterns of all species pairs for CNWR, FL.

Fish could be more readily captured in these types of habitats than in ponds or lakes. Wading birds in other locations selected habitats where there is a higher energy return rate (Hafner and Britton 1983; Kersten *et al.* 1991). Among Snowy Egrets and Tricolored Herons in Florida, the most important mechanism maintaining partitioning was different foraging efficiencies (Kent 1986).

Another explanation was that wading birds are using habitat in relation to what was available. In this study, I did not measure the availability of each habitat category and therefore I am unable to determine if species showed preferences for specific types of habitat or if they are merely using habitat categories in relation to their proportional availability.

Patterns within Regions

For the larger wading bird species, my results support the hypothesis that similar-sized species overlap in habitat use (Willard 1977). In all three regions, Great Egrets and Great Blue Herons had the highest overlap. Other researchers have found high overlap in habitat use among these species as well. During the breeding season, Great Egrets and Great Blue Herons (along with Snowy Egrets) used inland freshwater sites in the mangrove swamps of the Yucatán peninsula (Ramo and Busto 1993). Overlap in habitat use between Great Blue Herons and Great Egrets in coastal marshes of New Jersey varied seasonally as species moved from saltwater to freshwater sites (Willard 1977). The sites in my study only had freshwater in the form of precipitation that fell and therefore, species may have had higher overlap in habitat use throughout the year than what Willard observed in New Jersey. For these two species, prey type and size seem to be important mechanisms of resource partitioning (Willard 1977; Hom 1983; Ramo and Busto 1993).

Research conducted at ANWR during the winter season of 1992-93 found that differently-sized herons had the highest overlap in habitat use(Chavez-Ramirez and Slack 1995). Two groups emerged, the Great Egret-Tricolored Heron-Reddish Egret group and the Snowy Egret-Great Blue Heron group (Chavez-Ramirez and Slack 1995). They suggested reasons for differences in their study and others may be related to differences between breeding and non-breeding season feeding requirements of wading bird species, prey movements into and out of the marsh or that wading birds that have high overlap in food resource use should have low overlap on another resource gradient, in this case habitat. This begs the question, why are my results different than theirs? Both my and Chavez-Ramirez and Slack's 1995 studies were conducted during the nonbreeding season and one might expect similar results. One reason for differences between the two studies may be due to variation in precipitation. Average rainfall for December 1996 (μ = 1.57) was lower than in December 1993 (μ = 2.31) when their study was conducted. Precipitation could, in turn, affect the amount of available open water habitat for the birds. During this study, habitats where wading birds were most often observed included vegetated areas, which is consistent with a reduction in open water habitat available. Conversely, perhaps differences between years could reflect wading birds selecting habitats where preferred food may be found. Herons rapidly shift foraging locations to match local and temporal prey abundance (Hafner *et al.* 1982; Hafner and Britton 1983; Kersten 1991).

CHAPTER IV

HABITAT USE AND HABITAT OVERLAP OF WINTERING WADING BIRDS AT TWO SITES ON THE TEXAS COAST

SYNOPSIS

I studied patterns of habitat use and overlap among wintering wading birds along the Gulf of Mexico coast. I report on interspecific differences in patterns of habitat use by an assemblage of wading birds at three different scales: macrohabitat, defined as the size of water body; mesohabitat or distance from land-water interface (i.e., edge); and microhabitat or water depth. I also compared patterns of habitat use by wintering wading birds between Matagorda Island National Wildlife Refuge (MINWR), Texas and Laguna Atascosa National Wildlife Refuge (LANWR), Texas. Based on ground surveys conducted over three winters of study, wintering wading birds partitioned foraging habitat at all three hierarchical levels. At the macrohabitat level, wintering wading birds showed interspecific differences in macrohabitat use of open water habitats. However, patterns of macrohabitat use varied among study sites. Wading birds foraging at MINWR occurred in cuts, lakes and vegetated flats ($\chi^2_{35} = 289.6$, $p < 0.001$), whereas at LANWR species were observed in lagoons, lakes and "channels" (a category that included both inlets and cuts) ($\chi^2_{28} = 258.5$, $p < 0.001$). Species which had high overlap in macrohabitat-use patterns used different foraging behaviors. At the mesohabitat level all species at MINWR used the category nearest the edge most often ($\chi^2_{35} = 245.2$, $p < 0.001$). At LANWR wading birds were observed most often in the mesohabitat category of 8.1-12 m. from the edge ($\chi^2_{24} = 198.0$, $p < 0.001$). At MINWR wading birds used water depth both <15 cm and from 16-

20 cm more often than expected (*K-S* test, $D = -265.3$, $p < 0.001$). All wading birds at LANWR also used water depths less than 15 cm more often than expected (*K-S* test, $D = -127.3$, $p < 0.001$). Great Egrets and Great Blue Herons at both locations were found in all water depth categories, whereas other species were not.

INTRODUCTION

Conservation and management plans for wading bird assemblages (i.e., herons, egrets, ibis and spoonbills) in North America have focused on the breeding season, despite evidence that the nonbreeding season is important to wading bird populations in Europe (Mikuska *et al.* 1998). For example, population stability of Grey Herons in Great Britain is affected by winter severity (Cave 1983). Likewise, conditions at wintering sites in West Africa affect population stability of Purple Herons (Held Den 1981). Nearly all North American heron populations are migratory (Hancock and Kushlan 1984) and the Gulf of Mexico coast has been identified as an area supporting significant numbers, or proportions of wintering wading birds (Mikuska *et al.* 1998). Despite this region's importance to wintering birds, few studies have focused on nonbreeding season habitat use along the Gulf of Mexico coast (but see Chavez-Ramirez and Slack 1995 and Dubowy 1996).

Conversely, many studies have documented habitat use by breeding wading birds. Previous studies have found that wading birds partition the habitat at a variety of scales. At the landscape or macrohabitat scale, wading birds utilize water bodies of differing in size (Chavez-Ramirez and Slack 1995) and salinity (Ramo and Busto 1993; Maccarone and Parsons 1994). Interspecific differences in macrohabitat utilization may also be due to different types or sizes of prey available among differently-sized water bodies, or behavioral interactions, such as

territoriality, that constrain habitat use by individuals (Kushlan 1976a). At the mesohabitat scale, some species partition habitat across a terrestrial-aquatic distance gradient (Frederick and Bildstein 1992). At the finest or microhabitat scale, water depth or tidal level most strongly influences patterns of wading bird habitat utilization (Meyerriecks 1962; Kushlan 1976a) (Custer and Osborn 1978a; Hom 1983; Maccarone and Parsons 1994; Austin 1996).

For management and conservation purposes, information is needed within key areas regarding the intraspecific and interspecific differences in habitats used during the nonbreeding season by wading birds (Mikuska *et al.* 1998). The importance of winter condition has been recognized to be important to wading bird populations in Europe, influencing populations of Grey Herons and Purple Herons (Held Den 1981; Cave 1983). Food limitation during the nonbreeding season can negatively impact body condition, thereby affecting breeding success the following season (Martin 1987). Therefore, knowledge of winter season foraging ecology can contribute to an understanding of specific breeding parameters required by a species (Frederick and Bildstein 1992). Better knowledge of the prey base can help to maintain or increase existing populations of wading birds.

Whereas there has been considerable research on wading bird foraging behavior during the breeding season (Kushlan 1978; Hafner 1997), little research has been conducted on the wintering grounds where the birds are under different environmental and physiological constraints. Factors unique to the nonbreeding season may alter foraging habitat use of wading birds, but this has not been examined. Specifically, the objectives of this study were to 1) determine interspecific differences in habitat use by wintering wading birds at three different scales: macrohabitat, mesohabitat and microhabitat scales; 2) to compare these differences across regions; 3) to determine overlap in macrohabitat use.

METHODS

Study Areas

I studied wading bird use of salt marsh habitats at two different sites along the Gulf of Mexico coast in Texas. The first site was Matagorda Island National Wildlife Refuge (MINWR), located in the coastal bend region of Texas, Calhoun County (Fig. 4.1). The refuge is a barrier island, 62 km long that varies from 1.2 to 7.3 km wide. Salt marsh areas were located on the west side of the island and consisted of vegetated flats dominated by glasswort, saltwort, sea-oxeye daisy, wolfberry, saltgrass, smooth cordgrass, and wind tidal flats dominated by mudlfat grass, saltgrass and cordgrasses. Interspersed among vegetated areas are bodies of open-water of varying sizes (Chavez-Ramirez and Slack 1995).

The second site was Laguna Atascosa National Wildlife Refuge (LANWR), located on the southern coast of Texas in Willacy and Cameron counties (Fig. 4.2). The refuge encompasses 182 km^2 and its eastern border is the Lower Laguna Madre of Texas. Laguna Atascosa National Wildlife Refuge is in a semi-arid, semi-tropical region which has aquatic habitat consisting of a mixture of freshwater lakes and ponds, brackish marshes and hypersaline lagoon waters. Saltmarsh vegetation consisted of a mixture of gulf cordgrass (*Spartina spartinae*), sedges (*Carex spp*., *Cyperus spp*.), rush (*Junicus spp*.), bulrush (*Scirpus spp*.), and saltgrass.

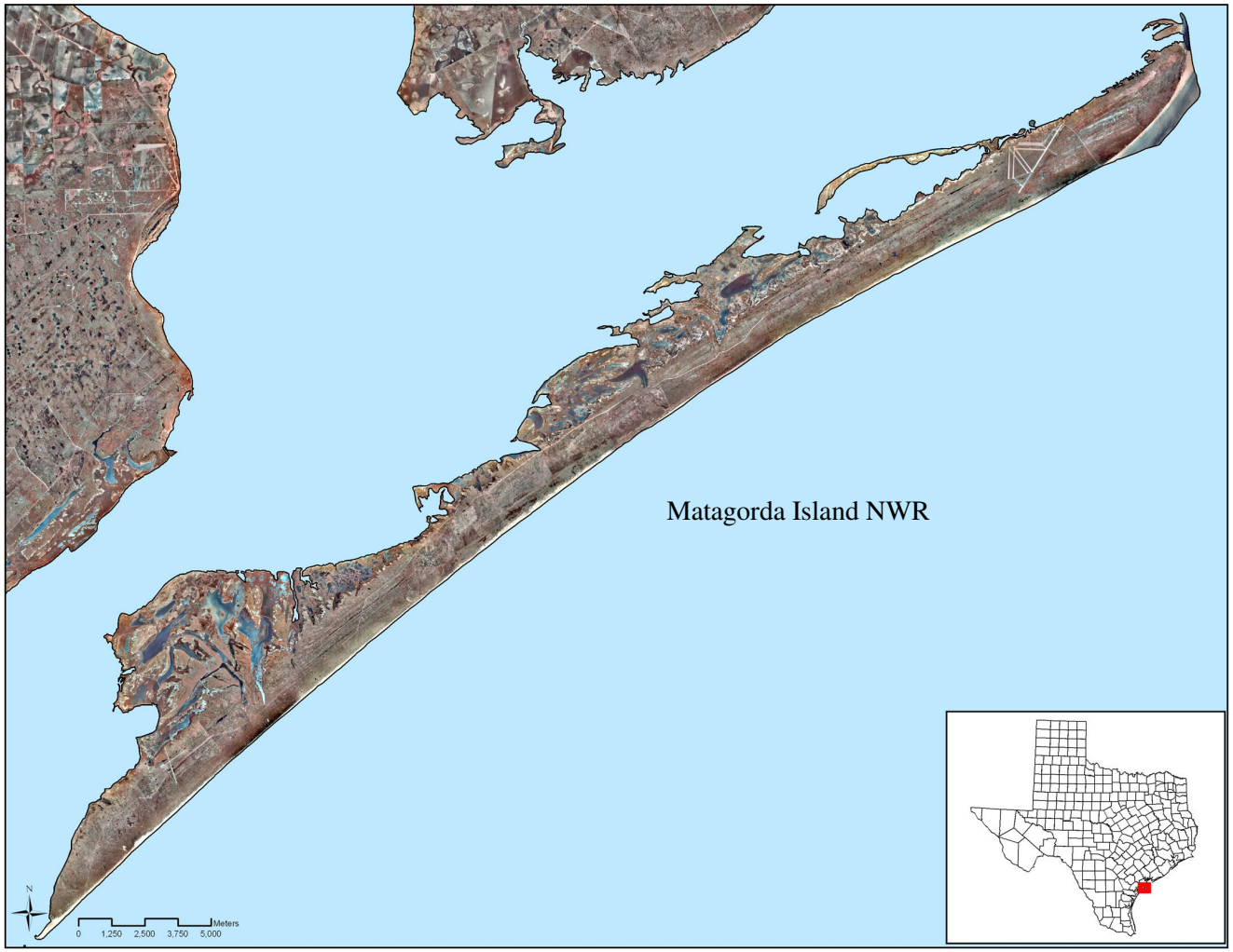

Figure 4.1. Map of MINWR, Texas.

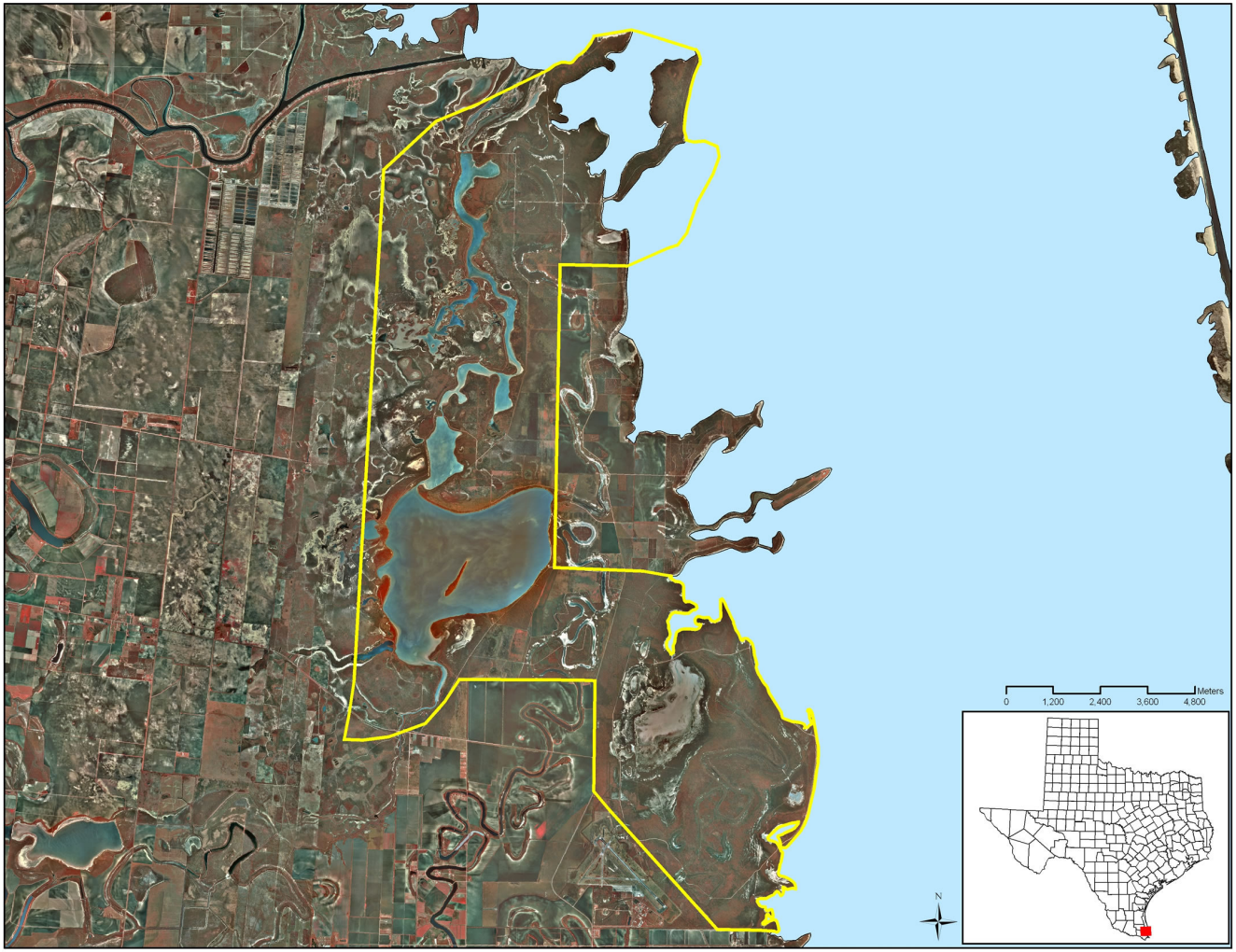

Figure 4.2. Map of LANWR, Texas.

Surveys

I conducted wading bird ground surveys at least once a month for a minimum of three consecutive days from 6 October 1997 through 28 March 1998 at MINWR, TX, and LANWR, TX, during daylight hours. From 16 October 1999 through 19 March 2000, wading bird ground surveys were conducted MINWR, TX once per month, for a minimum of two days during daylight hours. All surveys were conducted from a truck along roads adjacent to the marshes.

Surveys focused on the following species of wading birds: Great Blue Herons, Great Egrets, Snowy Egrets, Little Blue Herons, Reddish Egrets, Roseate Spoonbills and White Ibises. In order to determine the dispersion of flocks and individuals throughout the landscape, I classified wading bird foraging habitat into three hierarchical categories: macrohabitat (size of water body based on aerial or ground extent), mesohabitat (distance of individual to edge, i.e., land-water interface) and microhabitat (water depth) (Fig 4.3). Due to the shallow nature of the Gulf of Mexico coast, mesohabitat and microhabitat were examined separately. At the macrohabitat scale, I classified open-water habitat on the basis of ground extent and shape as follows: ponds (0-100m^2), lakes (>100m^2), bays (shallow open-water area adjacent to coast), cuts (narrow straight or winding, open-water areas connecting two or more bodies of water except bays) and inlets (same as cuts only connected on one end to a bay) (Chavez-Ramirez and Slack 1995). Another open-water habitat that was present at LANWR was the lagoon, which is a large (>100m^2) hypersaline waterbody.

Vegetated flat was the only non-open water macrohabitat category. An "other" category was added for analysis to include birds foraging in flooded tire tracks, culverts, land and unknown macrohabitat categories. I recorded individual birds, bird species and numbers within flocks, separately within each macrohabitat category. I estimated the perpendicular distance of each individual standing in water from the edge (i.e., interface between water and land). Mesohabitat categories were classified as follows for MINWR: 1) 0-2 m from land-water interface (edge); 2) 2.1-4 m from edge; 3) 4.1-6 m from edge and so on as necessary. Due to small sample sizes in some categories, I collapsed the mesohabitat categories for LANWR into: 1) 0-4 m; 2) 4.1-8 m; 3) 8.1-12 m.; and >12 m.

When possible, water depth was measured immediately following wading bird observations. Presence of vegetation, water temperature and salinity were also noted. When it was not possible to measure water depth, microhabitat was estimated in relation to the size of the foraging bird's leg. In this case, microhabitat categories were classified as follows: 1) water depth covered 1/3 leg length; 2) water depth covered 2/3 leg length; 3) water depth covered entire leg length. Microhabitat categories were then converted to water depth categories (0-15 cm; 16-30 cm and >30 cm) by comparison with leg measurements of heron specimens (Recher and Recher 1972; Willard 1977; Hom 1983).

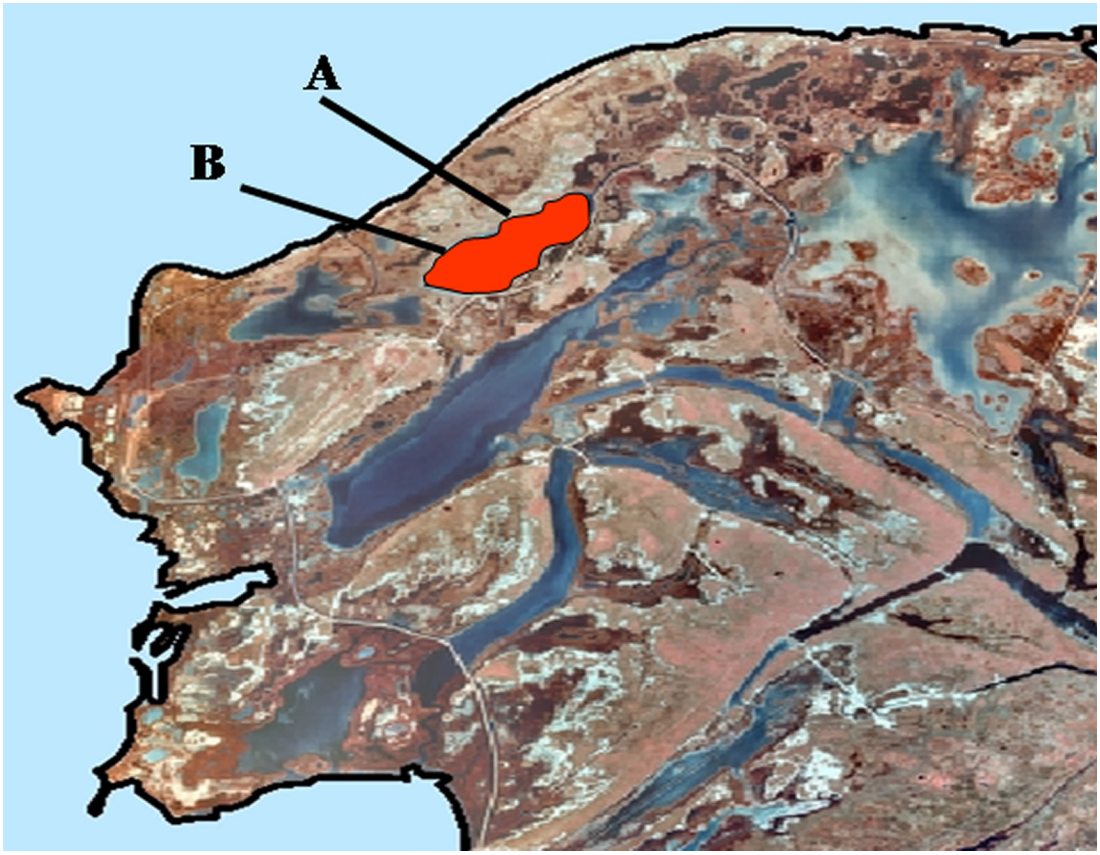

Figure 4.3. Schematic showing A) macrohabitat-defined as ground extent of open-water habitat and B) mesohabitat-defined as an estimate of the perpendicular distance of an individual wading bird from the edge (or land-water interface).

Analyses

Overall differences (total abundance of all species) in habitat use among categories within macro- and mesohabitat categories were evaluated using a Chi-Square test (Conover 1980). Differences in the use of macro- and mesohabitat categories by individual species were evaluated with a Chi-square goodness-of-fit test (Conover 1980). I assumed that all macro, meso- and microhabitat categories were equally likely to be used. I calculated Pearson's correlation coefficients to determine if there was a significant relationship between distance from edge and water depth. Kolmogorov goodness of fit tests were used to evaluate differences in wading bird use of microhabitat categories both intra and interspecifically. I used the Kolmogorov-Smirnov goodness of fit test to determine if species were using all water depth categories based on the assumption that all habitat categories were equally available. I also used the Kolmogorov-Smirnov goodness of fit tests to make individual comparisons between the distribution of each species to all others.

I calculated niche overlap using Pianka's niche overlap index (Pianka 1973) for each pair of species:

$$O_{12} = O_{21} = \frac{\sum_{i=1}^{n} (p_{2i})(p_{1i})}{\sqrt{\sum_{i=1}^{n} (p_{2i})^2 (p_{1i})^2}}$$

Where p_{1i} and p_{2i} represent the proportions of the *i*th resource used by the 1st and 2nd species respectively. And the overlap of species one on species two (O_{12}) and overlap of species two on one (O_{21}) are symmetric or equal. This equation can generate values between zero or one with the higher the niche overlap the closer the index is to one (Pianka 1979). Dendrograms were built (average method) using the overlap indexes between species.

RESULTS

Macrohabitat

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The eight most common species observed on ground surveys were Snowy Egrets (*N* = 339), Great Egrets (*N* = 235) , Roseate Spoonbills (*N* = 79) , White Ibises (*N* = 68), Tricolored Herons (*N* = 54) , Reddish Egrets (*N* = 39), Little Blue Herons (*N* = 30) and Great Blue Herons (*N* = 24) for a total of (*N* = 868). Patterns of wading bird macrohabitat use were significantly different among species (χ^2_{35} = 289.6, $p < 0.001$) (Fig. 4.4). All species showed differences in the types of macrohabitats that they used (Table 4.1). An "other" category was added for analysis to include birds foraging in flooded tire tracks (*N* = 66), culverts (*N* = 1), land (*N* = 1) and unknown macrohabitat categories (*N* = 35). Great Egrets occurred more often than expected in

cuts and vegetated flats, while ponds, lakes and inlets were used less often than expected (χ^2_5 = 118.2, $p < 0.001$) (Fig.4.5 A). Snowy Egrets were observed more than expected in lakes (χ^2_5 = 93.6, $P < 0.001$) and less than expected in ponds, lakes, inlets, cuts and vegetated flats (Fig. 4.5 B). Tricolored Herons were found most often in vegetated flats and cuts ($\chi^2_5 = 31.3$, $p < 0.001$) and less often than expected in ponds, lakes and inlets (Fig. 4.6 A). Reddish Egrets were most common in cuts ($\chi^2_5 = 18.3$, $p < 0.01$) (Fig. 4.6 B), and used vegetated flats and ponds less often than expected. White Ibises used vegetated flats and cuts more often than expected and ponds, inlets and lakes less than expected ($\chi^2_5 = 31.2$, $p < 0.001$) (Fig. 4.7 A). Roseate Spoonbills used ponds and inlets more than expected ($\chi^2_5 = 43.2$, $p < 0.001$), lakes as expected and cuts and vegetated flats less than expected (Fig. 4.7 B). Little Blue Herons used inlets, cuts and lakes more than expected, occurred less often than expected in vegetated flats and none were seen in ponds ($\chi^2_5 = 20.8$, $p < 0.001$) (Fig. 4.8 A). Great Blue Herons used cuts and to a lesser extent vegetated flats and lakes ($\chi^2_5 = 16.0$, $p < 0.01$) (Fig. 4.8 B). Inlets were used less often than expected by Great Blue Herons and none were observed in ponds (Fig. 4.8 B).

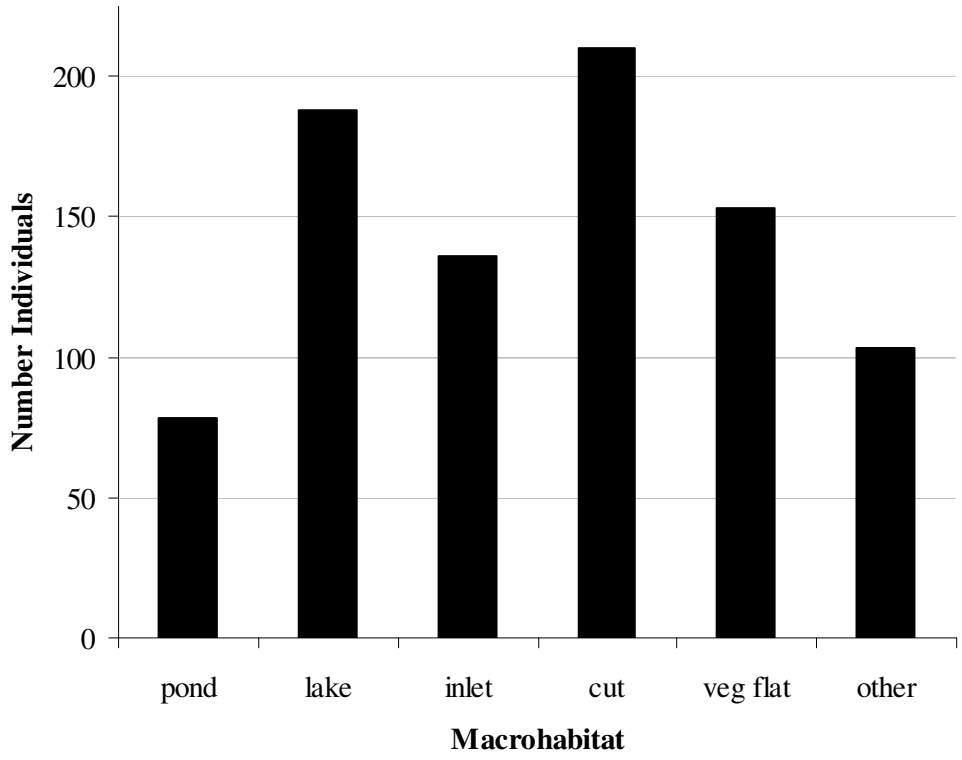

Figure 4.4. Patterns of macrohabitat use by all species of wintering wading birds combined (*N* = 868) at MINWR Texas during 1997-2000 fall and winter.

Table 4.1. Number of wading bird species observed and expected in different macrohabitats in Texas coastal salt marsh MINWR during 1997-2000 fall and winter. Expected frequencies are for Chi-square goodness-of-fit tests for each species separately, based on the assumption that all habitat categories were equally accessible.

	Macrohabitat Categories						
Species	**Pond**	**Lake**	**Inlet**	**Cut**	**Veg Flat**	**Other**	**N**
Great Egret	20	22	36	98	42	17	235
Expected	39.2						
Snowy Egret	24	117	43	42	47	66	339
Expected	56.5						
Tricolored Heron	1	5	8	13	22	5	54
Expected	9.0						
Reddish Egret	1	7	8	15	5	3	39
Expected	6.5						
White Ibis	3	10	6	13	27	9	68
Expected	11.3						
Roseate Spoonbill	29	14	21	11	3	1	79
Expected	13.2						
Little Blue Heron	0	8	11	8	2	1	30
Expected	5.0						
Great Blue Heron	0	5	3	10	5	1	24
Expected	4.0						

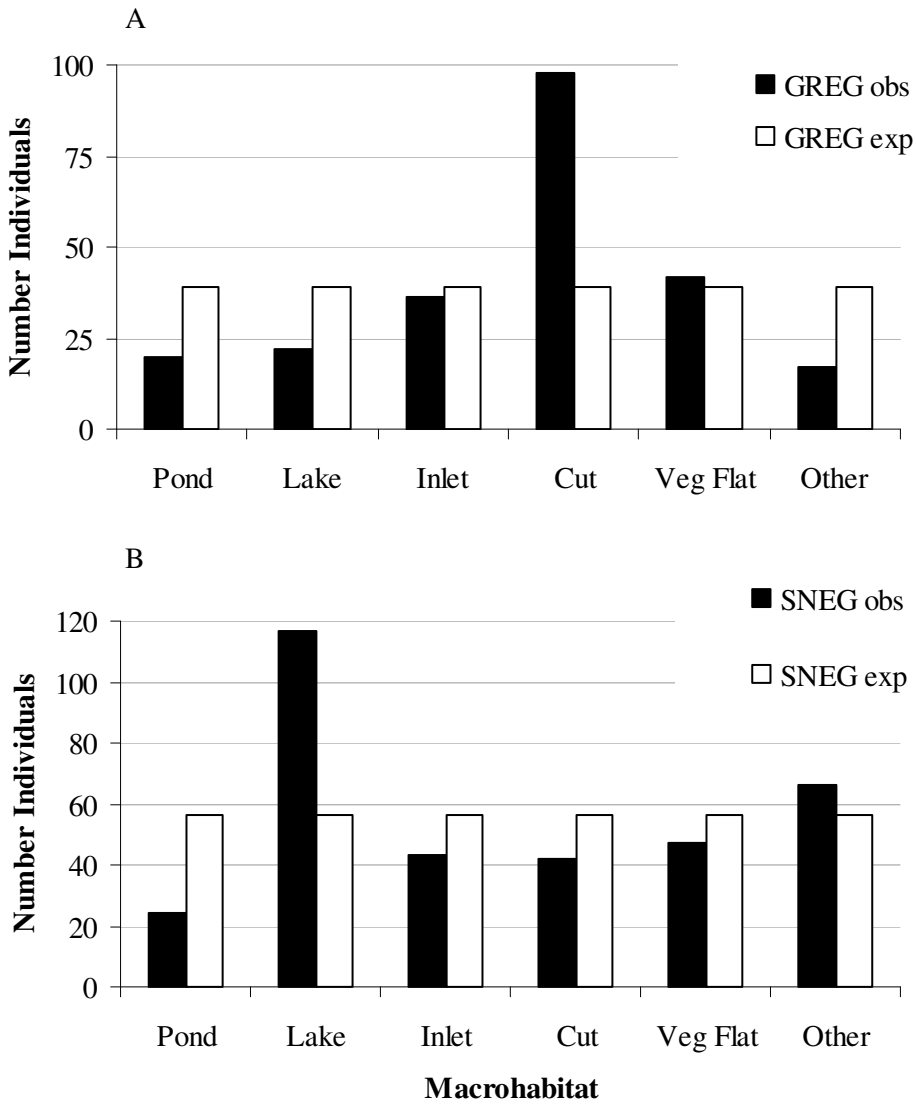

Figure 4.5. A) Patterns of macrohabitat use by Great Egrets (*N* = 235) and B) Snowy Egrets (*N* = 339) at MINWR, TX during 1997-2000 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

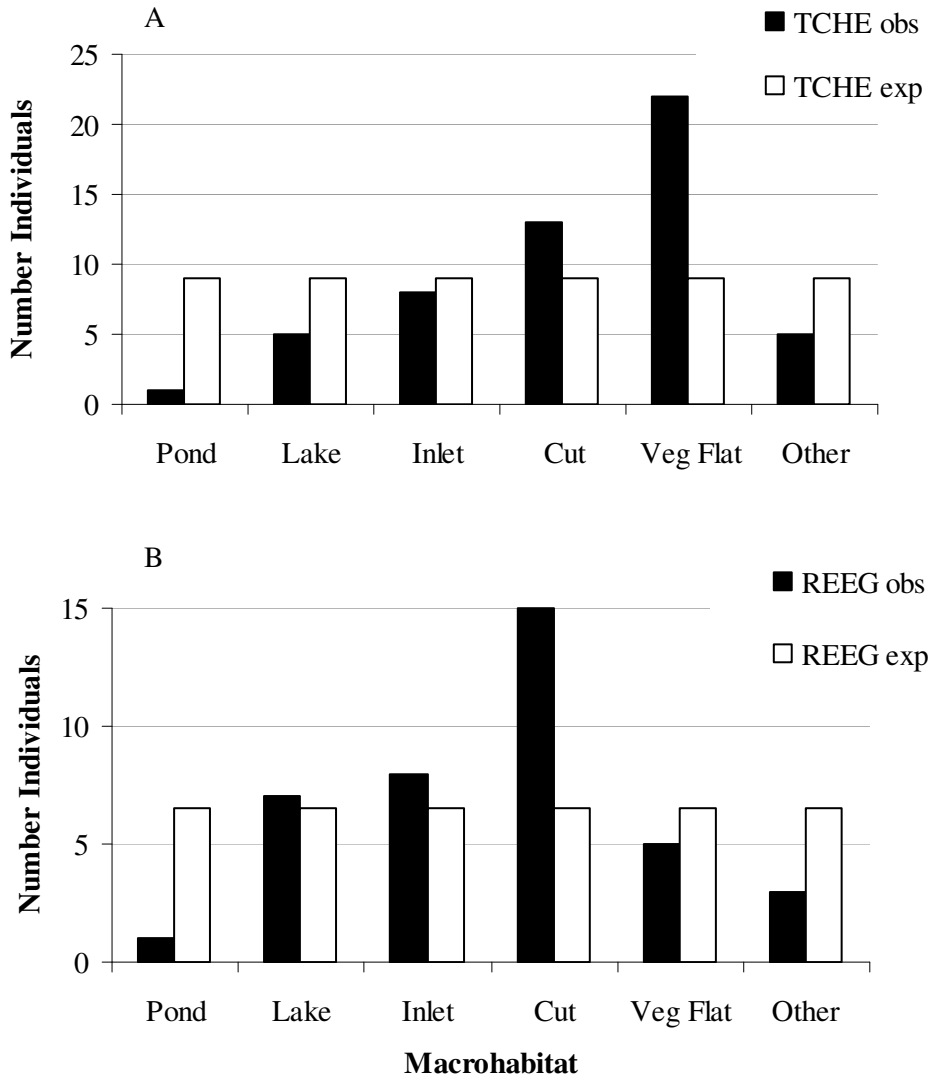

Figure 4.6. A) Patterns of macrohabitat use by Tricolored Herons (*N* = 54) and B) Reddish Egrets (*N* = 39) at MINWR, TX during 1997-2000 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

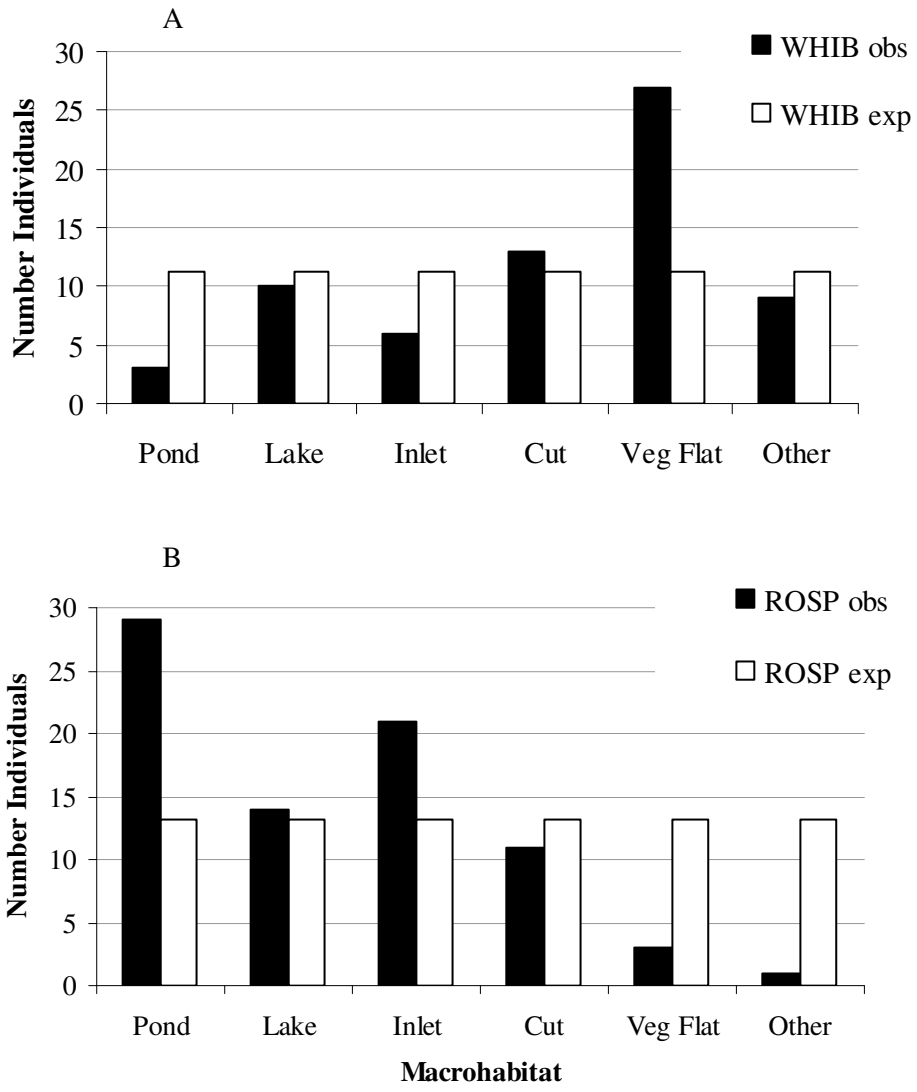

Figure 4.7. A) Patterns of macrohabitat use by White Ibises (*N* = 68) and B) Roseate Spoonbills (*N* = 79) at MINWR, TX during 1997-2000 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

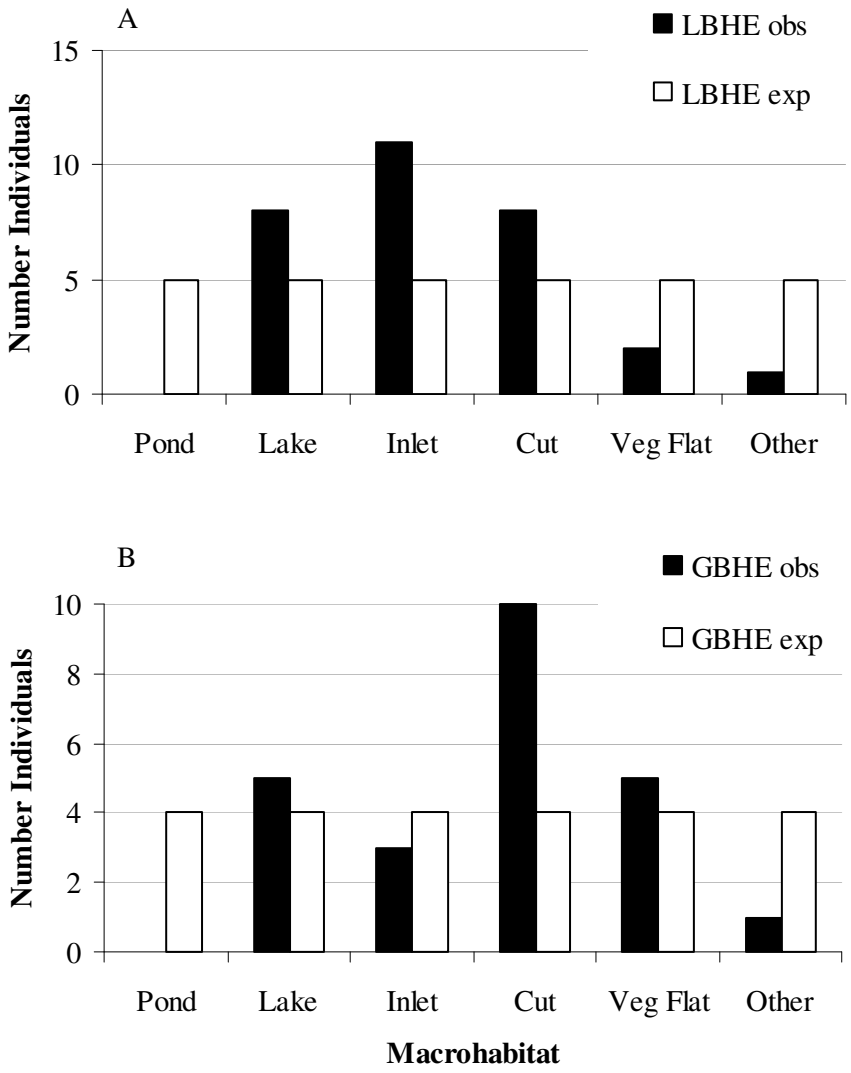

Figure 4.8. A) Patterns of macrohabitat use by Little Blue Herons (*N* = 30) and B) Great Blue Herons (*N* = 24) at MINWR during 1997-2000 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

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During the fall/winter of 1998-1999, I observed the same species at LANWR, Texas: Snowy Egrets (N = 66), Great Egrets (N = 53), Roseate Spoonbills (N = 76), White Ibises (N = 122), Tricolored Herons (N = 28), Reddish Egrets (N = 21), Little Blue Herons (N = 19) and Great Blue Herons (N = 8). Patterns of wading bird macrohabitat use here were also significantly different among species (χ228=258.5, P < 0.001) (Table 4.2, Fig. 4.9). Because of small sample sizes, inlets and cuts were combined into single category called "channel" for analysis. Great Egrets ($\chi^2_4 = 70.7$, $p < 0.001$) occurred more often than expected in lakes and lagoons and less often than expected in ponds, channels and bays (Fig. 4.10 A). Snowy Egrets preferred channels and lagoons ($\chi^2_4 = 57.0$, $p < 0.001$) (Fig. 4.10 B). They occurred to a lesser extent in ponds, lakes and bays. Lagoons also were preferred by Tricolored Herons, which occurred as expected or less than expected in all other categories ($\chi^2_4 = 22.3$, $p < 0.001$) (Fig.4.11 A). Reddish Egrets were observed more often than expected in lakes and much less often than expected in all other categories ($\chi^2_4 = 35.4$, $p < 0.001$) (Fig. 4.11 B). White Ibises were most common in lagoons, lakes, channels and were rarely observed in bays or ponds ($\chi^2_4 = 73.0$, $p < 0.001$) (Fig. 4.12. A). Roseate Spoonbills only used lagoons and lakes and were not observed in other macrohabitat categories ($\chi^2_4 = 161.5$, $p < 0.001$) (Fig 4.12. B). Ponds and lakes were used most often by Little Blue Herons ($\chi^2_4 = 13.3$, $p < 0.01$) (Fig 4.13. A). There was no significant difference in macrohabitat use by Great Blue Herons ($\chi^2_4 = 7.1$, $p > 0.01$) (Fig. 4.13. B).

Table 4.2. Number of wading bird species observed and expected in different habitats in Texas coastal salt marsh LANWR during 1998-1999 fall and winter. Expected frequencies are for Chi-square goodness-of-fit tests for each species separately, based on the assumption that all habitat categories were equally accessible.

	Macrohabitat Categories					
Species	**Pond**	**Lake**	**Channel**	**Bay**	**Lagoon**	**N**
Great Egret	0	33	1	5	14	53
Expected	10.6					
Snowy Egret	2	5	31	3	25	66
Expected	13.2					
Tricolored Heron	2	6	4	1	15	28
Expected	5.6					
Reddish Egret	2	15	2	0	2	21
Expected	4.2					
White Ibis	2	39	36	1	44	122
Expected	24.4					
Roseate Spoonbill	0	19	0	0	57	76
Expected	15.2					
Little Blue Heron	9	6	2	1	1	19
Expected	3.8					
Great Blue Heron	2	4	0	2	0	8
Expected	1.8					

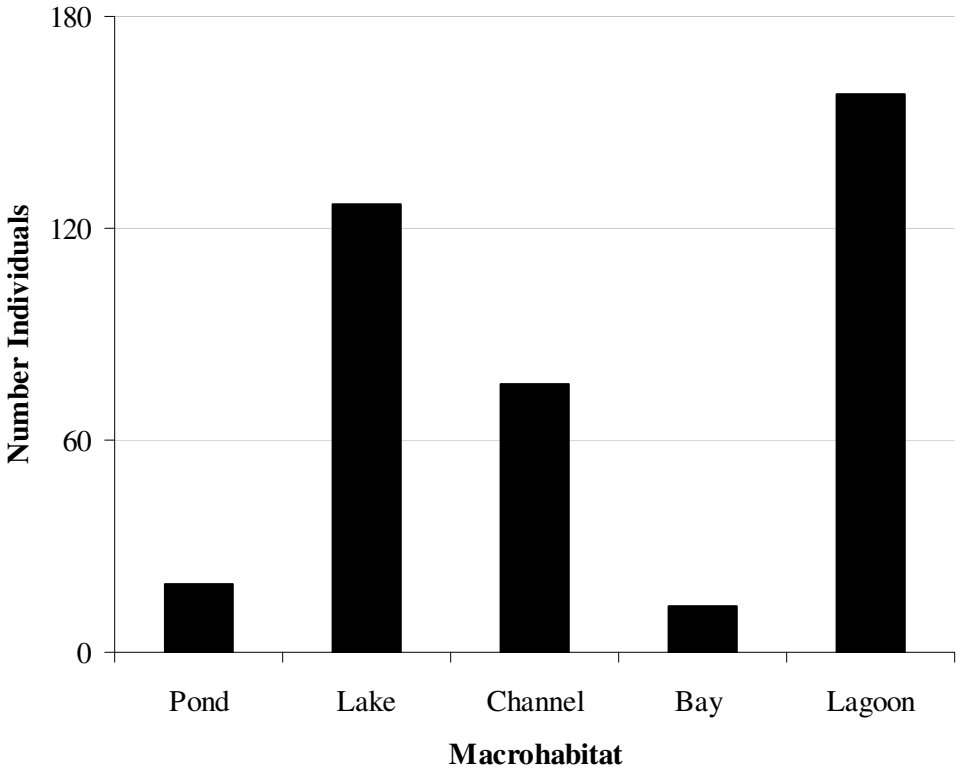

Figure 4.9. Patterns of macrohabitat use by wintering wading birds at LANWR (*N* = 393) during 1998-1999 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

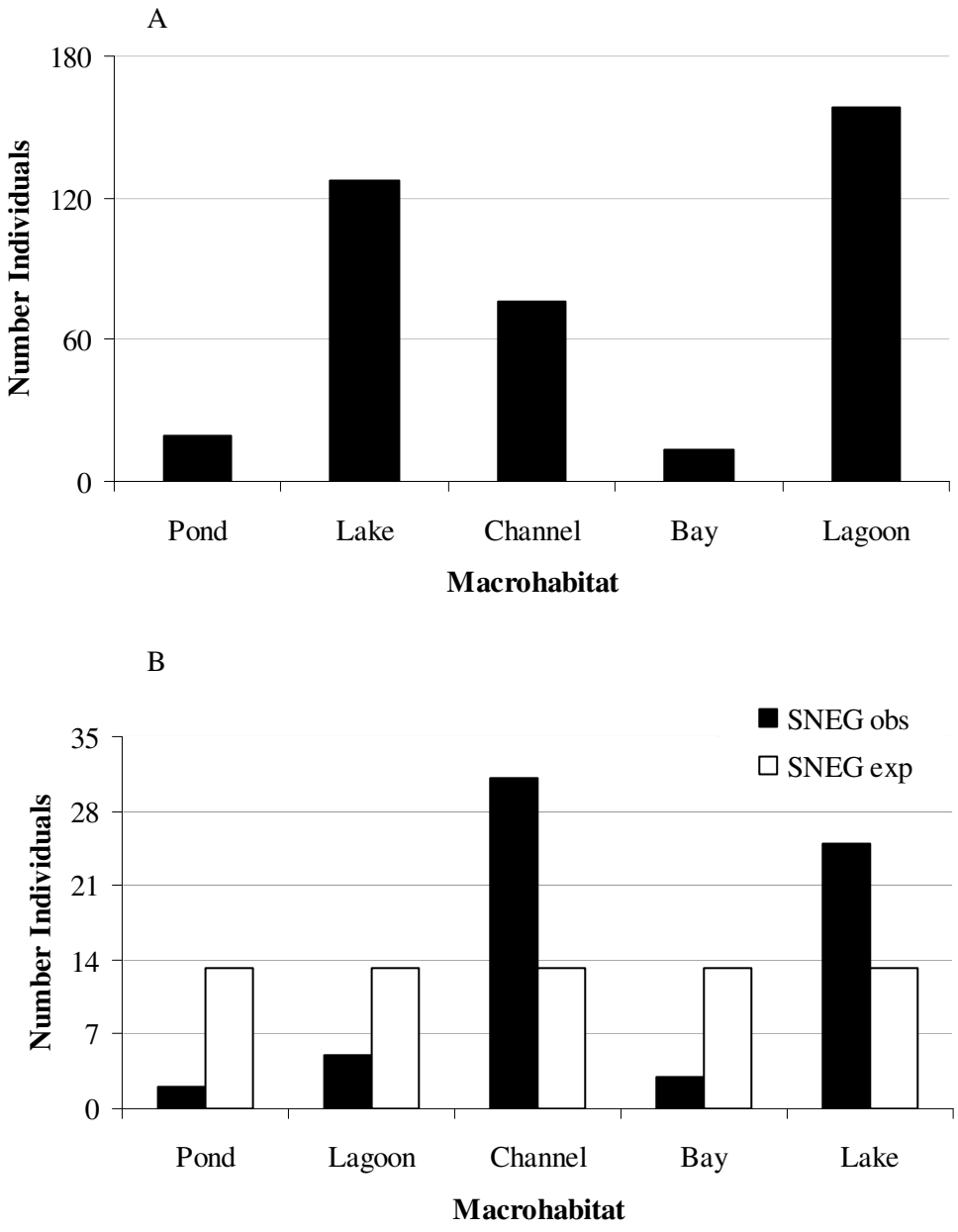

Figure 4.10. A) Patterns of macrohabitat use by Great Egrets (*N* = 53) at LANWR during 1998-1999 fall and winter. B) Patterns of macrohabitat use by Snowy Egrets (*N* = 66) at LANWR during 1998-1999 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

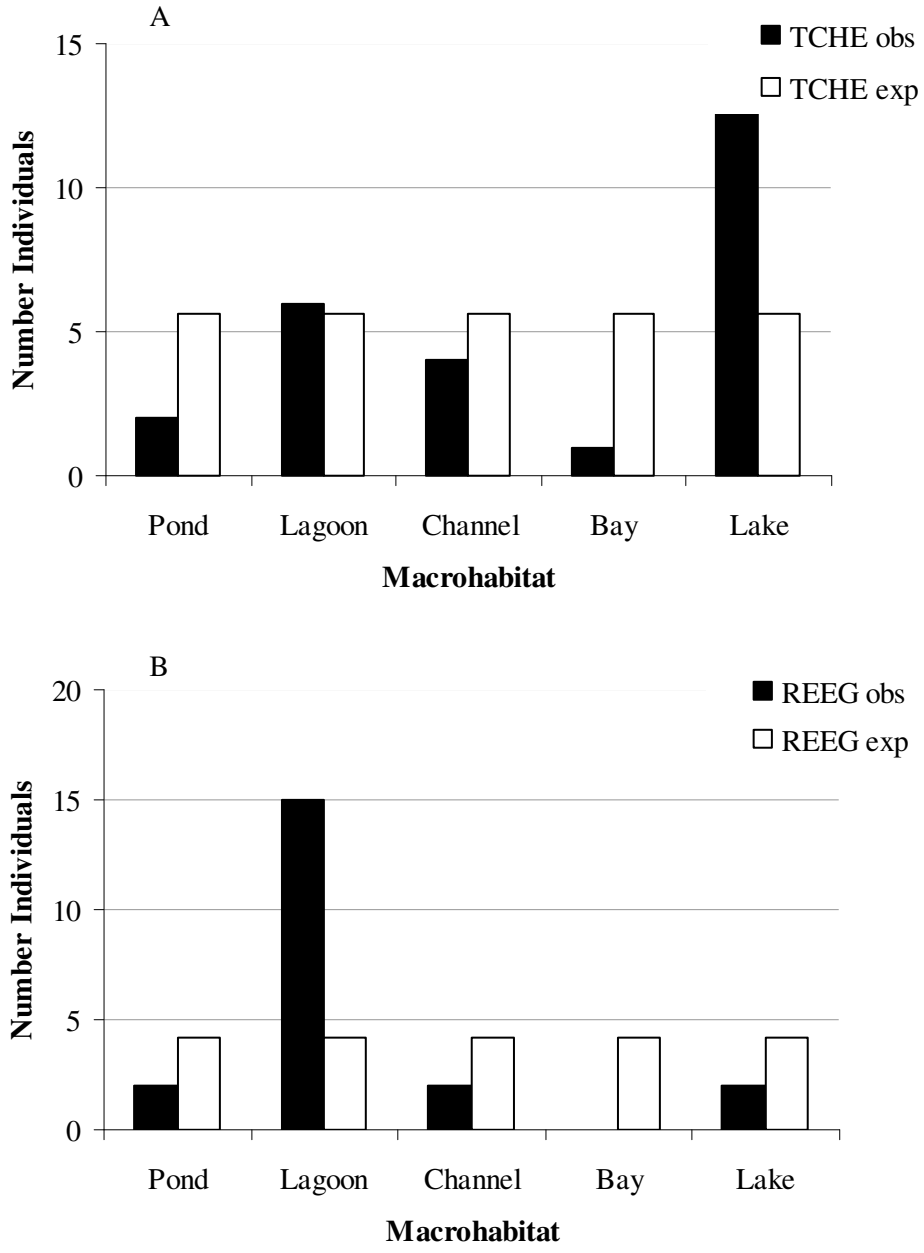

Figure 4.11. A) Patterns of macrohabitat use by Tricolored Herons (*N* = 28) at LANWR during 1998-1999 fall and winter. B) Patterns of macrohabitat use by Reddish Egrets (*N* = 21) at LANWR during 1998-1999 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

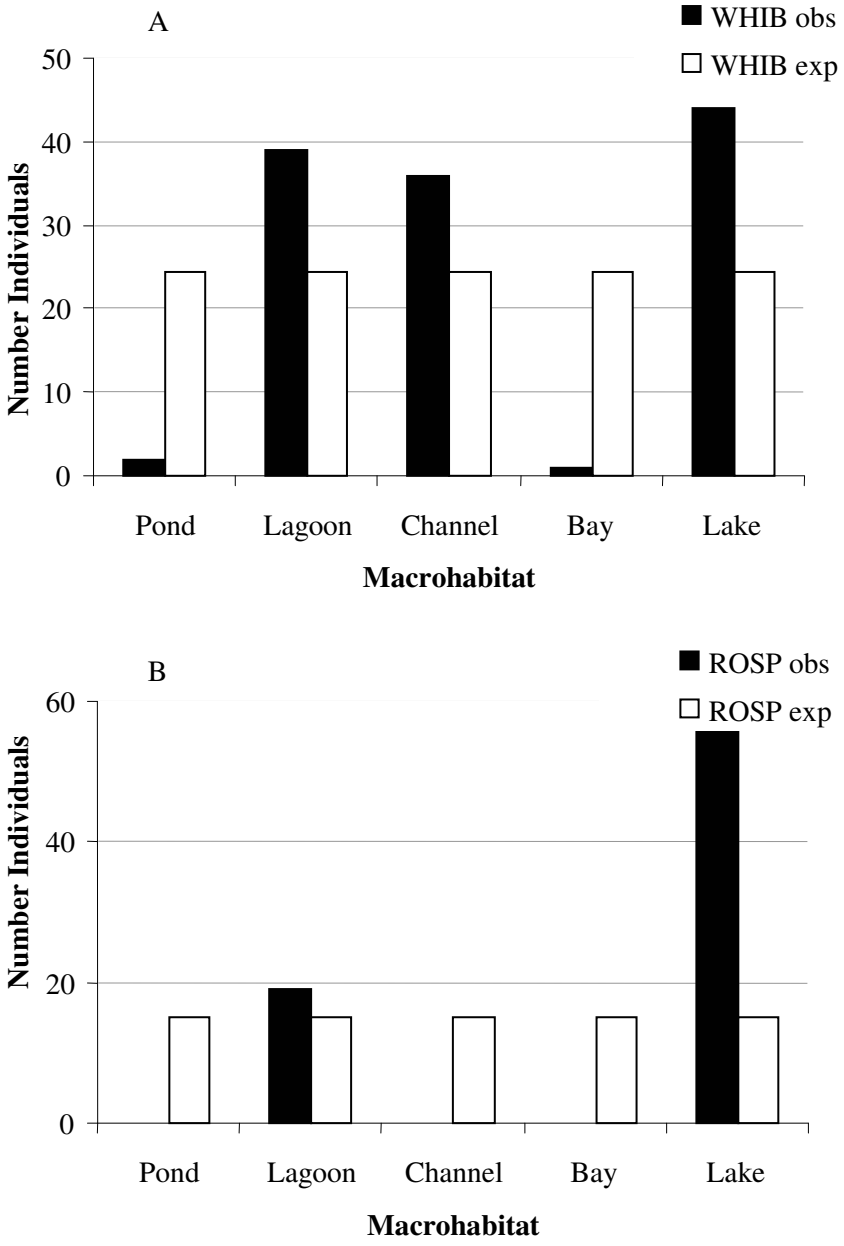

Figure 4.12. A) Patterns of macrohabitat use by White Ibises (*N* = 122) at LANWR during 1998-1999 fall and winter. B) Patterns of macrohabitat use by Roseate Spoonbills (*N* = 76) at LANWR during 1998-1999 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

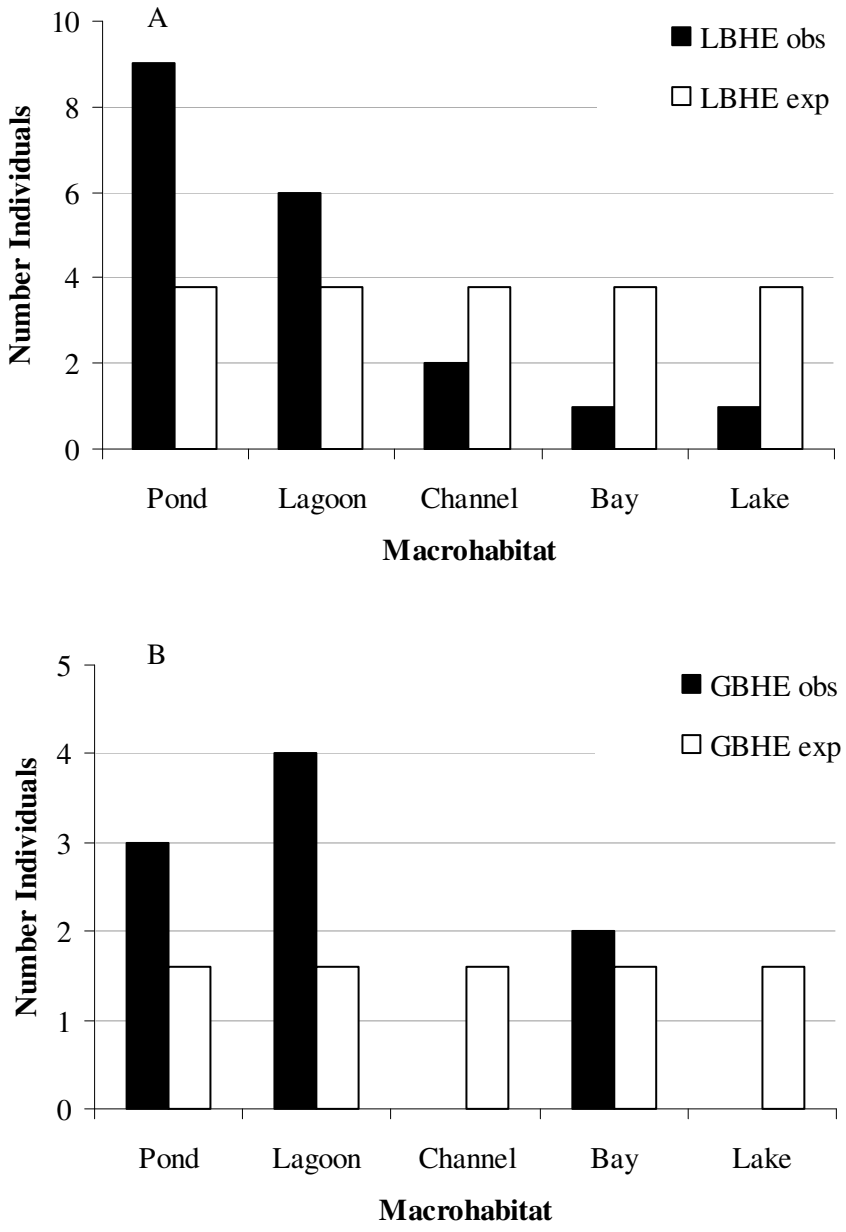

Figure 4.13. A) Patterns of macrohabitat use by Little Blue Herons (*N* = 19) at LANWR during 1998-1999 fall and winter. B) Patterns of macrohabitat use by Great Blue Herons (*N* = 8) at LANWR during 1998-1999 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

Overlap Indices

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I constructed a dendrogram based on Pianka niche overlap indices calculated for macrohabitat use patterns for all species and three different groups emerged (Fig. 4.14). The specific overlap index is based on a comparison of the resource utilization curves of the two species with values ranging from 0-1) (1 = complete overlap, while 0 = no overlap). The first group included White Ibis, Tricolored Herons, Great Blue Herons, Reddish Egrets and Great Egrets. Within this group, there was high niche overlap between White Ibises and Tricolored Herons (0.98) and Great Blue Herons, Reddish Egrets and Great Egrets (0.97). The next group included the small herons, Snowy Egrets and Little Blue Herons (0.72). Roseate Spoonbills overlapped the least with all other groups (0.56).

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Dendrograms constructed for macrohabitat use patterns of all species at Laguna Atascosa were different (Fig. 4.15). Three groups also emerged here. In the first group were Great Egrets and Reddish Egrets (0.94). The second group included Tricolored Herons, Roseate Spoonbills, Snowy Egrets and White Ibises (0.78). The group that overlapped the least with the others (0.56) included Little Blue Herons and Great Blue Herons.

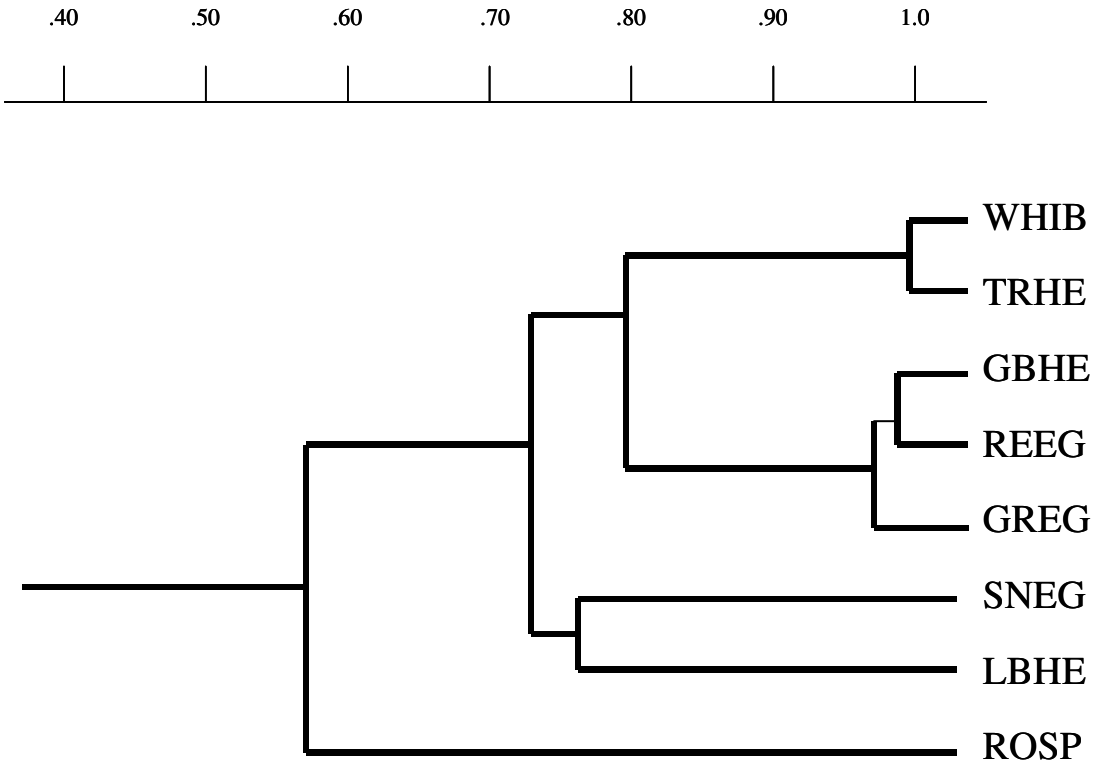

Figure 4.14. Dendrogram based on Pianka's niche overlap index calculated on macrohabitat use patterns of all species pairs at MINWR Texas. Specific overlap index is based on a comparison of the resource utilization curves of the two species with values ranging from 0-1: 1 = complete overlap, while 0 = no overlap.

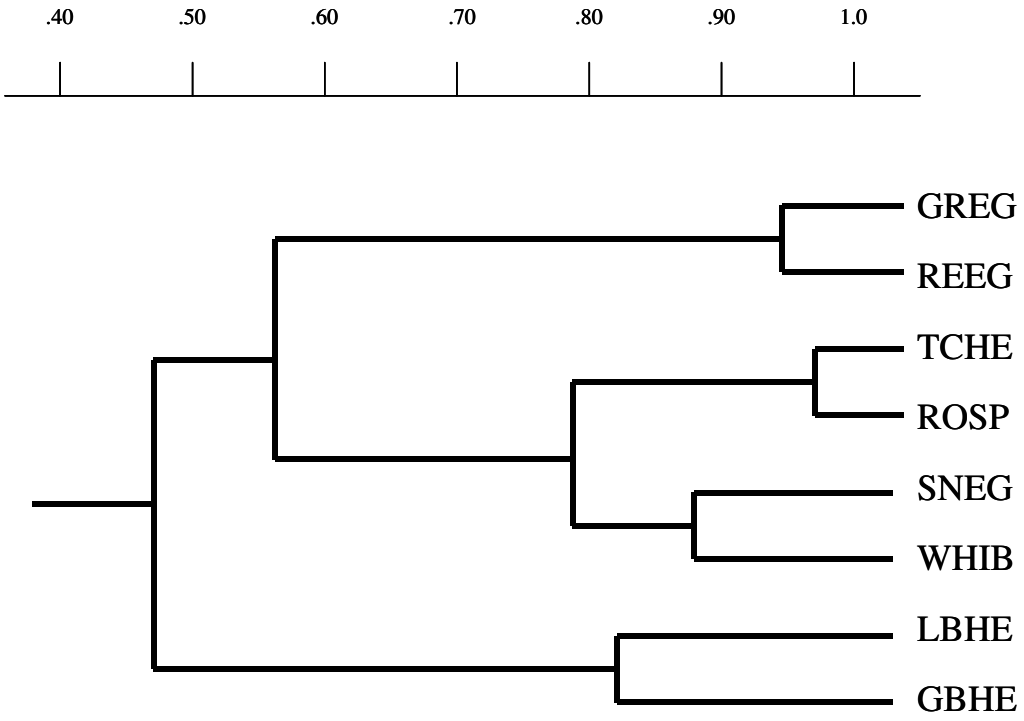

Figure 4.15. Dendrogram based on Pianka's niche overlap index calculated for all species pairs at LANWR Texas. Specific overlap index is based on a comparison of the resource utilization curves of the two species with values ranging from 0-1; 1 = complete overlap, while 0 = no overlap.

Mesohabitat

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I found no significant correlation between distance from edge and water depth ($N = 51$) (Pearson's Correlation: $r = –0.26$, *n.s.*). However, patterns of wading bird mesohabitat use were significantly different among species ($\chi^2_{35}=245.2$, $p < 0.001$) (Table 4.3, Fig. 4.16). All species were found 0-2 m from the edge more often than expected. Snowy Egrets were observed more often than expected in the 0-2 m category, whereas Great Egrets occurred more often in both the 0-2 m category and the 2.1-4 m. categories (Fig. 4.17. A, B). Tricolored Herons mesohabitat use was similar to Snowy Egrets and they were found more often than expected in the 0-2 m category, whereas Reddish Egrets, like Great Egrets were found more often than expected in both the 0-2 m and 2.1-4 m categories (Fig 4.18. A, B). White Ibises occurred more often than expected in the 0-2 m category, as expected in the 2.1-4 m category and they were not observed any further from the edge (Fig 4.19. A). Roseate Spoonbills had a pattern of mesohabitat use similar to White Ibises with the exception that they were observed as far out as 8.1-10 m from the edge (Fig 4.19. B). Little Blue Herons were found almost exclusively in the 0-2 m category, although they did occur in the 2.1-4 m category less than expected (Fig 4.20. A). And finally, like other wading birds, Great Blue Herons occurred most often in the 0-2 m from the edge category, however they were also observed in categories ranging out as far as >10 m from the edge (Fig 4.20. B).

Table 4.3. Number of wading bird species observed and expected in different mesohabitat categories (meters from edge) in Texas coastal salt marsh MINWR during 1997-2000 fall and winter. Expected frequencies are for Chi-square goodness-of-fit tests for each species separately, based on the assumption that all habitat categories were equally accessible.

	Distance From Edge (m)						
Species	**0-2**	**2.1-4**	**4.1-6**	**6.1-8**	**8.1-10**	**>10**	**N**
Great Egret	134	45	0	5	9	0	193
Expected	32.2						
Snowy Egret	172	18	3	42	44	0	279
Expected	46.5						
Tricolored Heron	25	5	2	0	0	0	32
Expected	5.3						
Reddish Egret	13	12	6	4	2	0	37
Expected	6.2						
White Ibis	47	11	0	0	0	0	58
Expected	9.7						
Roseate Spoonbill	51	12	0	0	10	0	73
Expected	12.2						
Little Blue Heron	29	1	0	0	0	0	30
Expected	5.0						
Great Blue Heron	16	2	1	2	0	2	23
Expected	3.8						

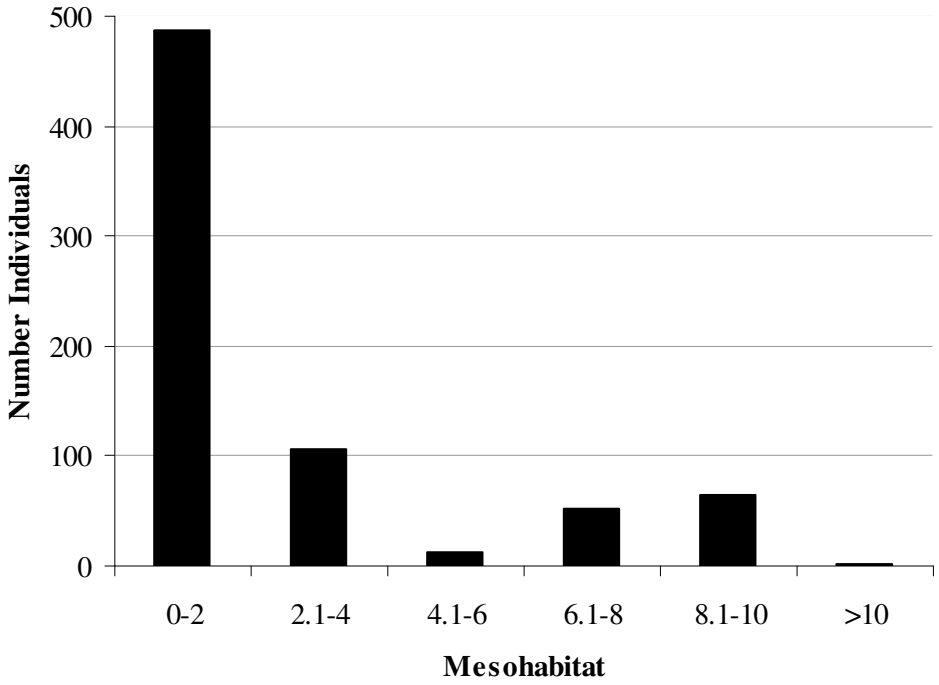

Figure 4.16. Overall wading bird mesohabitat use at MINWR Tx during 1997-2000 fall and winter (*N* = 725).

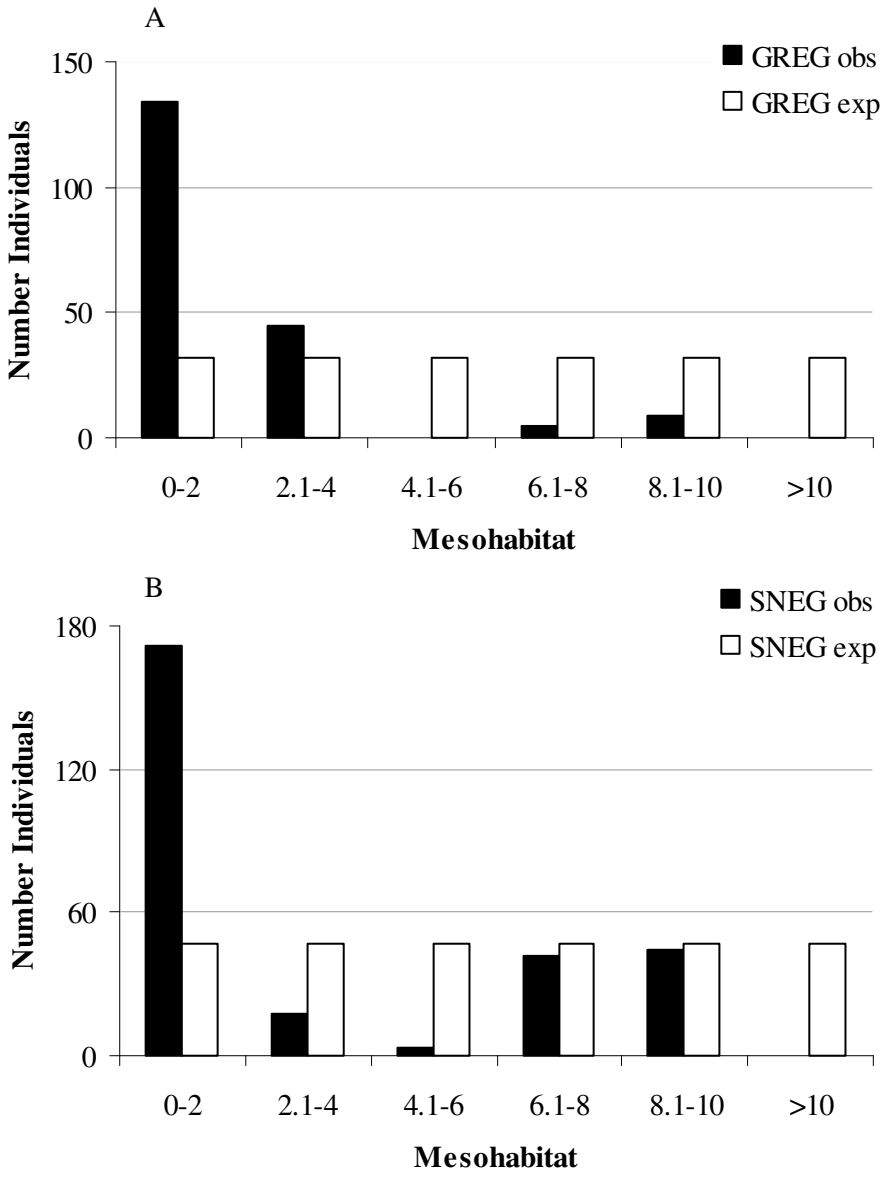

Figure 4.17. A) Patterns of mesohabitat use by Great Egrets (*N* = 193) and B) by Snowy Egrets (*N* = 279) at MINWR, Texas during 1997-2000 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

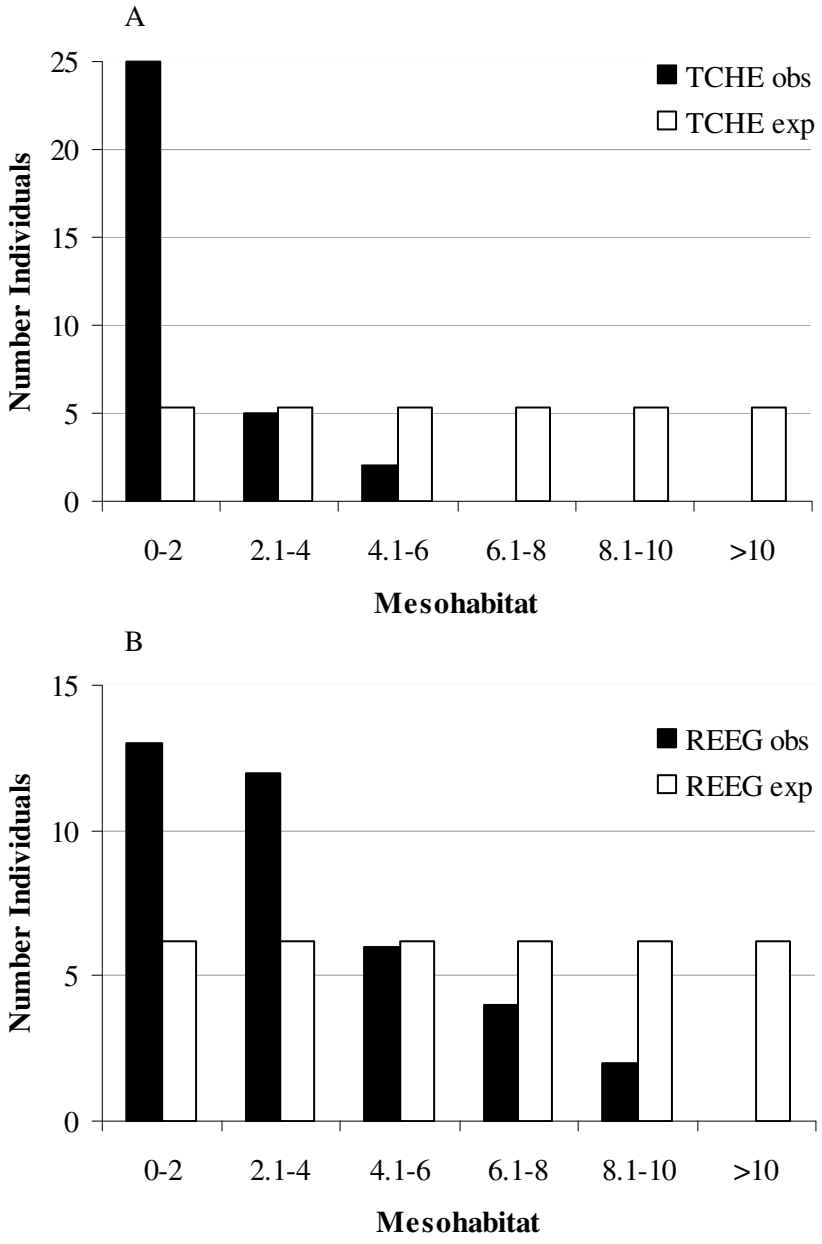

Figure 4.18. A) Patterns of mesohabitat use by Tricolored Herons (*N* = 32) and B) by Reddish Egrets (*N* = 37) at MINWR, Texas during 1997-2000 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

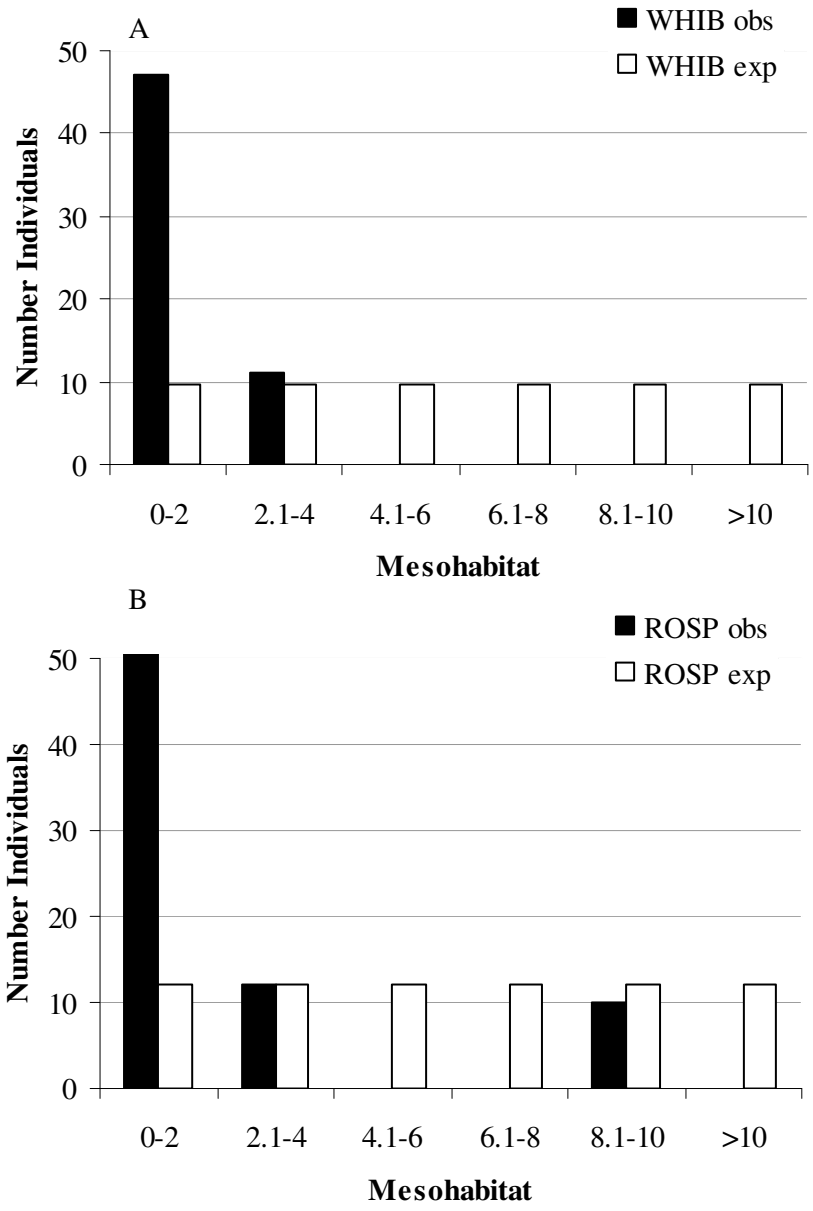

Figure 4.19. A) Patterns of mesohabitat use by White Ibises (*N* = 58) and B) Roseate Spoonbills (*N* = 73) at MINWR, TX during 1997-2000 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

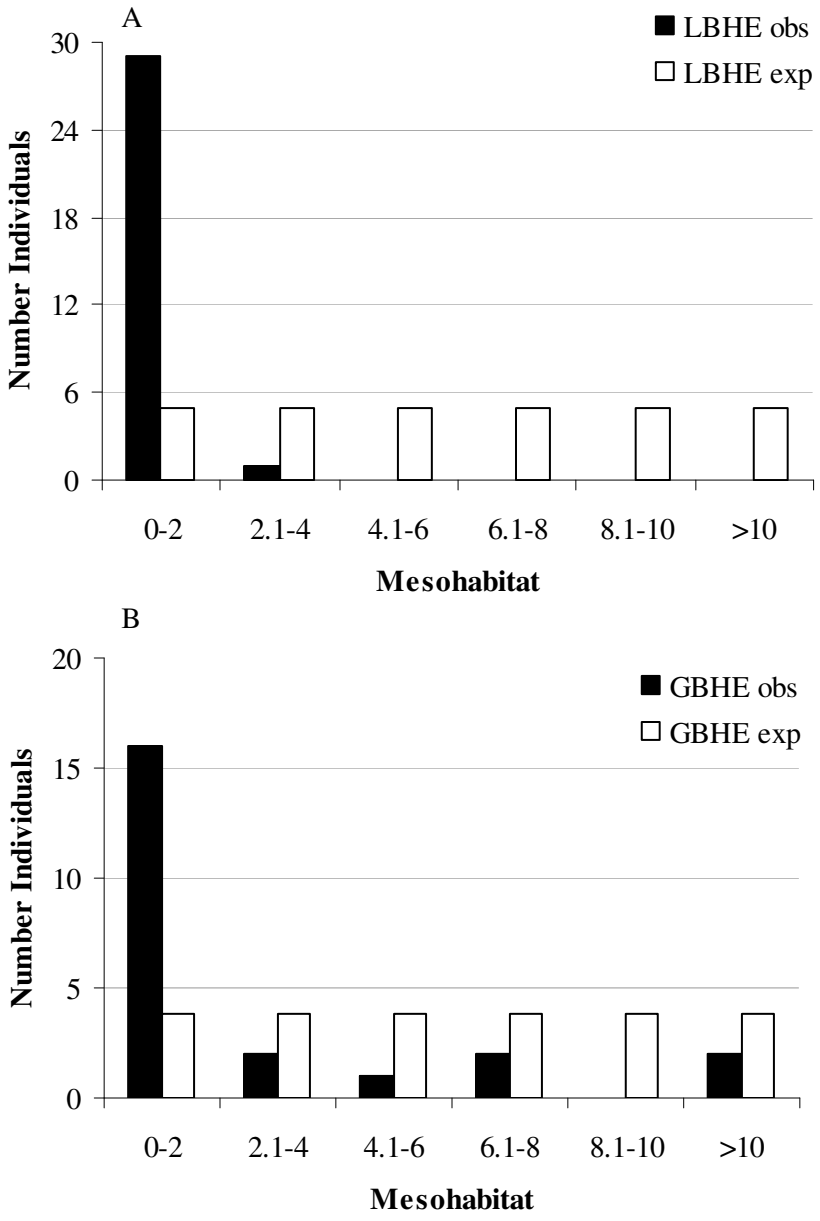

Figure 4.20. A) Patterns of mesohabitat use by Little Blue Herons (*N* = 30) and B) by Great Blue Herons (*N* = 23) at MINWR, Texas during 1997-2000 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

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Overall patterns of mesohabitat use were significantly different among species at LANWR (χ^2_{24}=198.0, $p < 0.001$) (Table 4.4, Fig. 4.21). There was a positive correlation between distance from edge and water depth (N = 29) (Pearson's r =0.41, $p < 0.05$), nevertheless, all birds were generally found further from the edge than at MINWR. Because sample sizes were too small in mesohabitat categories that varied by two meter increments (e.g., 0-2 m, 2.1-4 m, etc.), I collapsed mesohabitat categories for Laguna Atascosa into 4 meter increments (e.g., 0-4 m, 4.1-8 m, etc.). Great Egrets were observed more often than expected in the category farthest from the edge (>12.1), as expected in the 8.1-12 m category and less than expected in the 0-4 and 4.1-8 m categories (Fig 4.22. A). Snowy Egrets occurred much more often than expected in the 0-4 m category and, slightly more often than expected in the 8.1-12 m category and less than expected in other categories (Fig 4.22. B). Tricolored Herons occurred more often than expected in the 8.1-12 m category and to a lesser extent in the 0-4 m category. They occurred less often than expected in the >12.1 m category (Fig 4.23. A). Reddish Egrets were observed more often than expected in both the 0-4 m and >12.1 m categories (Fig 4.23 B). White Ibises were seen more often than expected in three categories, 0-4 m, 8.1-12 m and >12.1 m (Fig 4. 24. A). Whereas Roseate Spoonbills were observed more often than expected only in the 8.1-12 m category and as expected in the > 12.1 m category (Fig. 4.24. B). Little Blue Herons were observed much more often than expected in the 0-4 m. category, slightly more often than expected in the >12.1 m category and less often than expected in the other categories (Fig. 4.25. A). Great Blue Herons were observed more often than expected in the >12.1 m category as well as in the 0-4 m category (Fig. 4.25. B).

Table 4.4 Number of wading bird species observed and expected in different mesohabitat categories (meters from edge) in Texas coastal salt marsh LANWR during 1998-1999 fall and winter. Expected frequencies shown here are for Chi-square goodness-of-fit tests for each species separately, based on the assumption that all habitat categories were equally accessible.

Species	**0–4**	**4.1–8**	**8.1–12**	**>12.1**	***N***
Great Egret	7	0	13	34	54
Expected	13.5				
Snowy Egret	41	1	20	5	67
Expected	16.8				
Tricolored Heron	9	0	13	6	28
Expected	7				
Reddish Egret	11	0	3	7	21
Expected	5.3				
White Ibis	41	0	43	38	122
Expected	30.5				
Roseate Spoonbill	0	0	57	19	76
Expected	19				
Little Blue Heron	11	2	0	6	19
Expected	4.8				
Great Blue Heron	3	0	0	6	9
Expected	2.3				

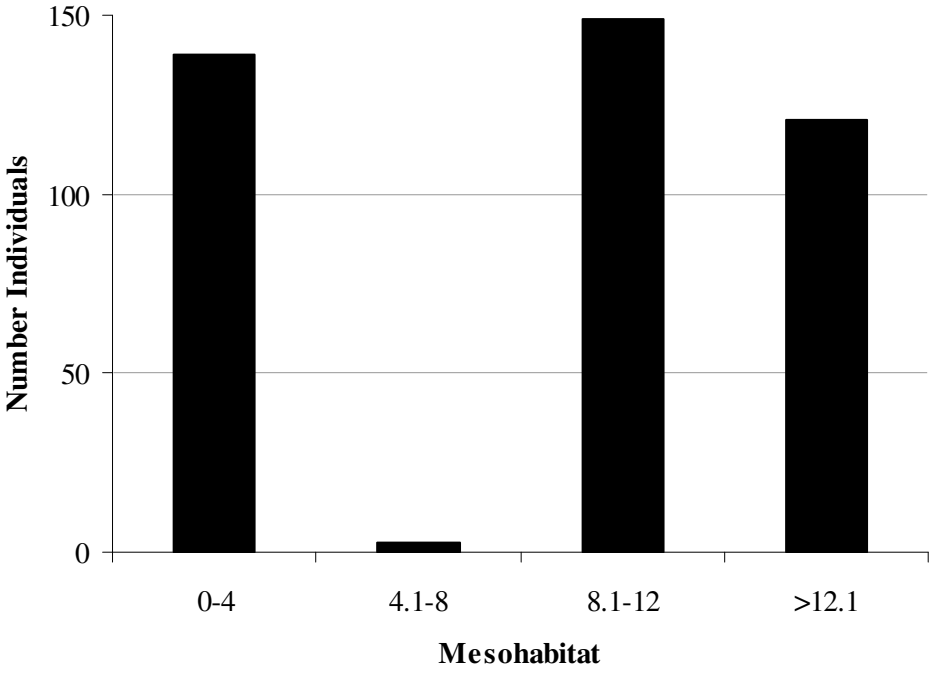

Figure 4.21. Overall wading bird mesohabitat use at LANWR Texas 1998-1999 during fall and winter (*N* =412).

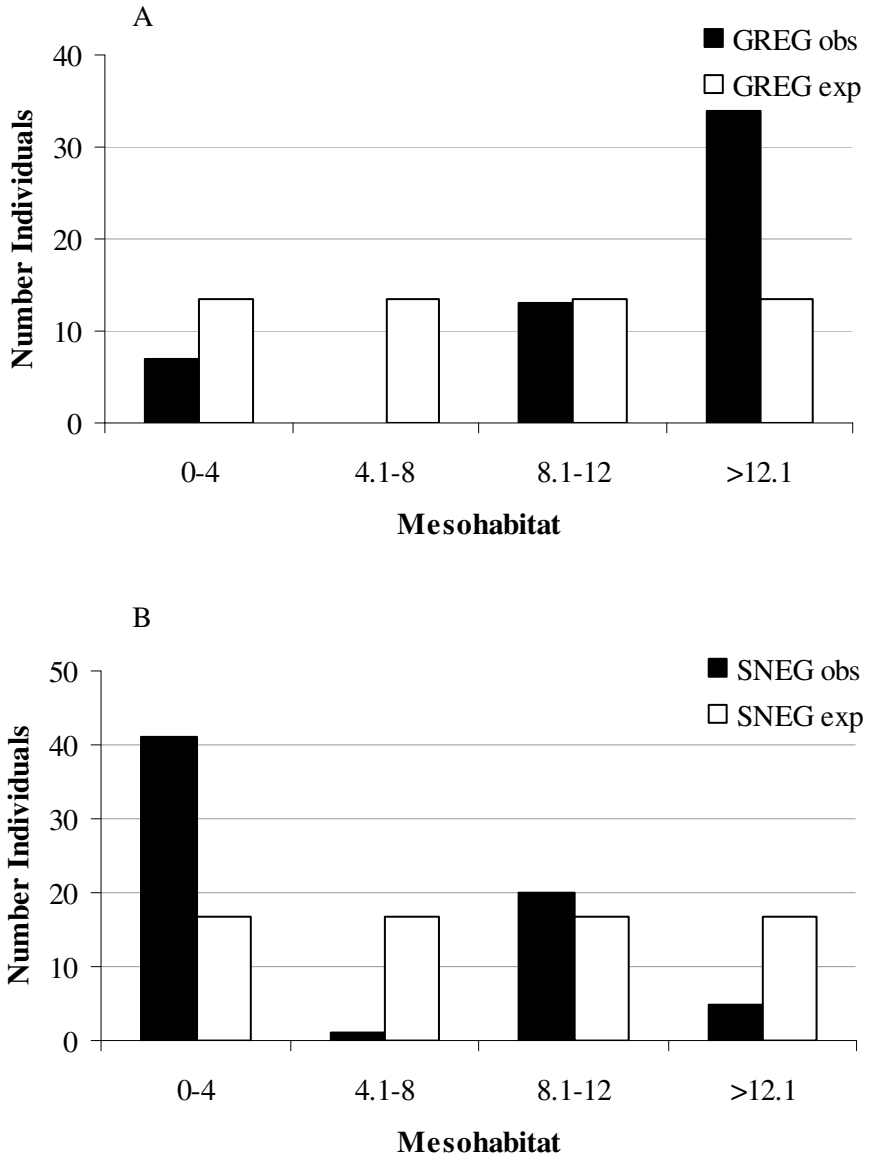

Figure 4.22. A) Patterns of mesohabitat use by Great Egrets (*N* = 54) and B) by Snowy Egrets (*N* = 67) at LANWR, Texas during 1998-1999 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

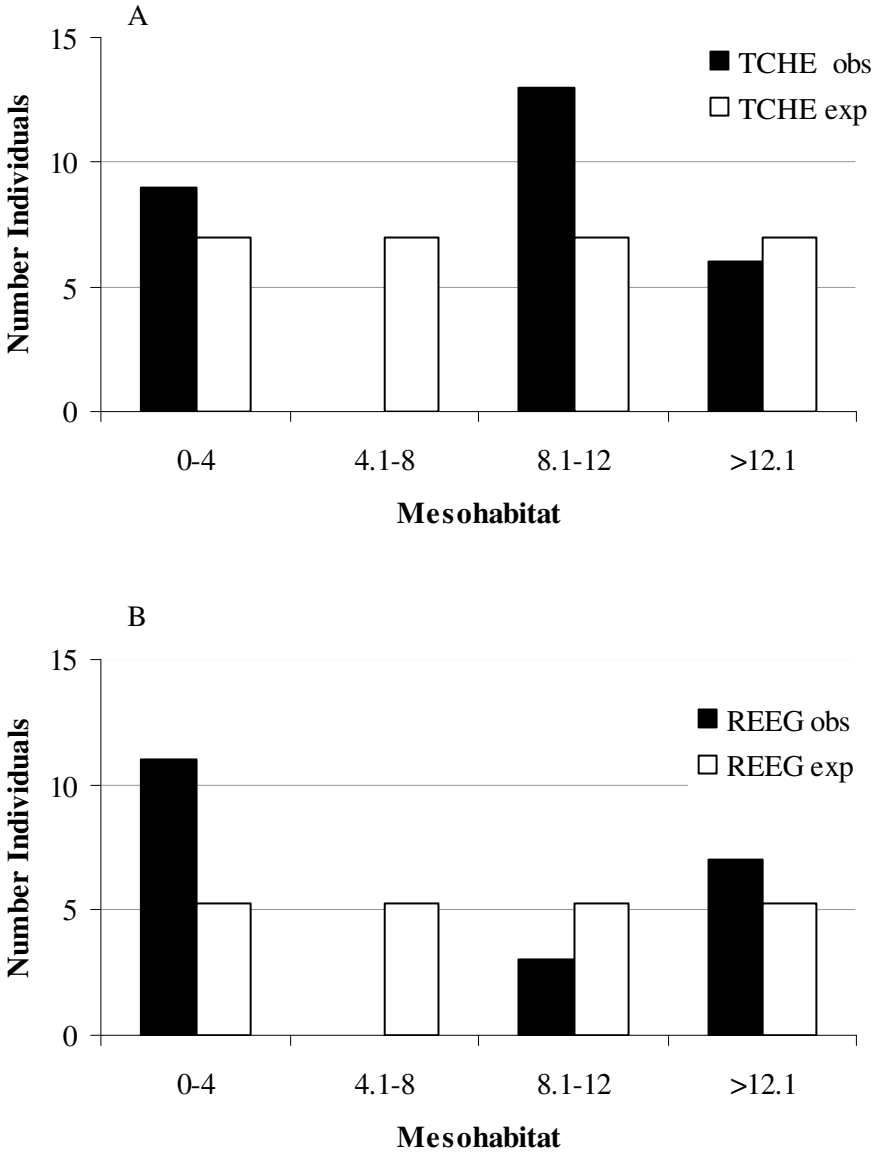

Figure 4.23. A) Patterns of mesohabitat use by Tricolored Herons (*N* = 28) and B) by Reddish Egrets (*N* = 21) at LANWR, Texas during 1998-1999 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

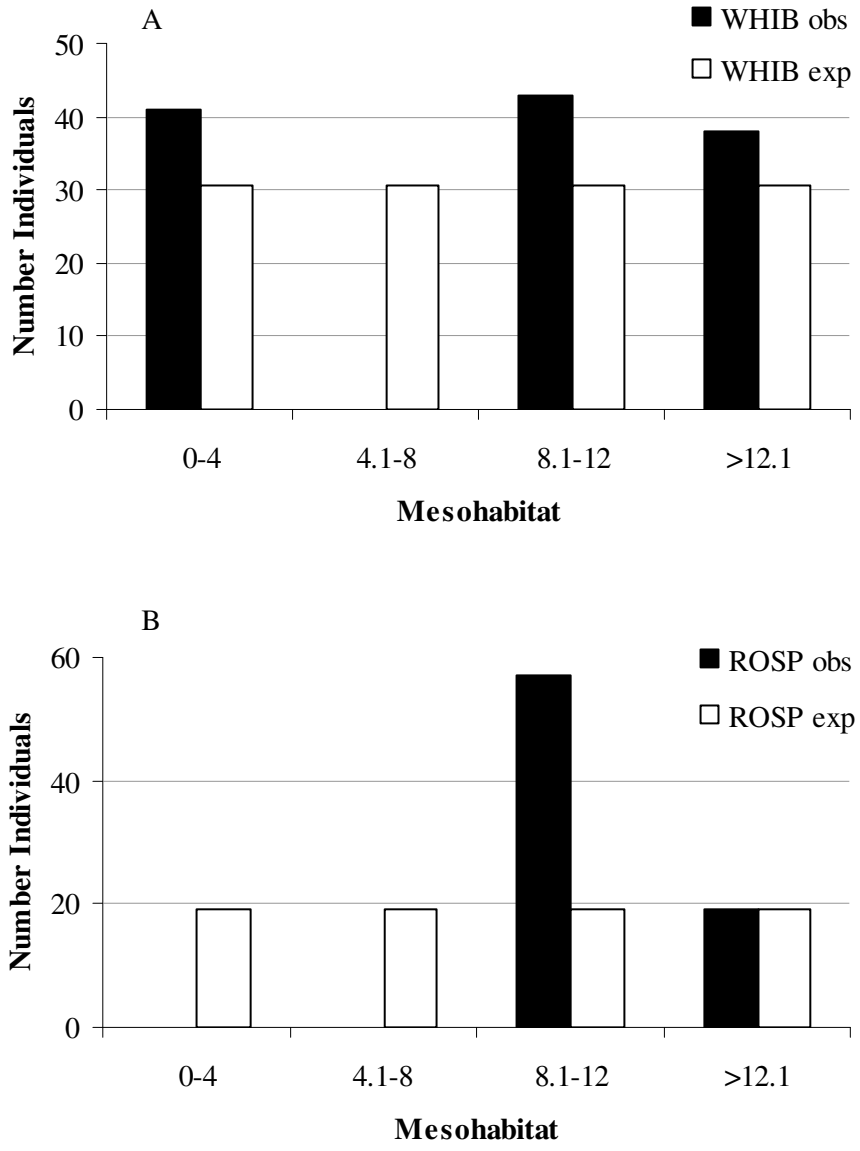

Figure 4.24. A) Patterns of mesohabitat use by White Ibises (*N* = 122) and B) by Roseate Spoonbills (*N* = 76) at LANWR, Texas during 1998-1999 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

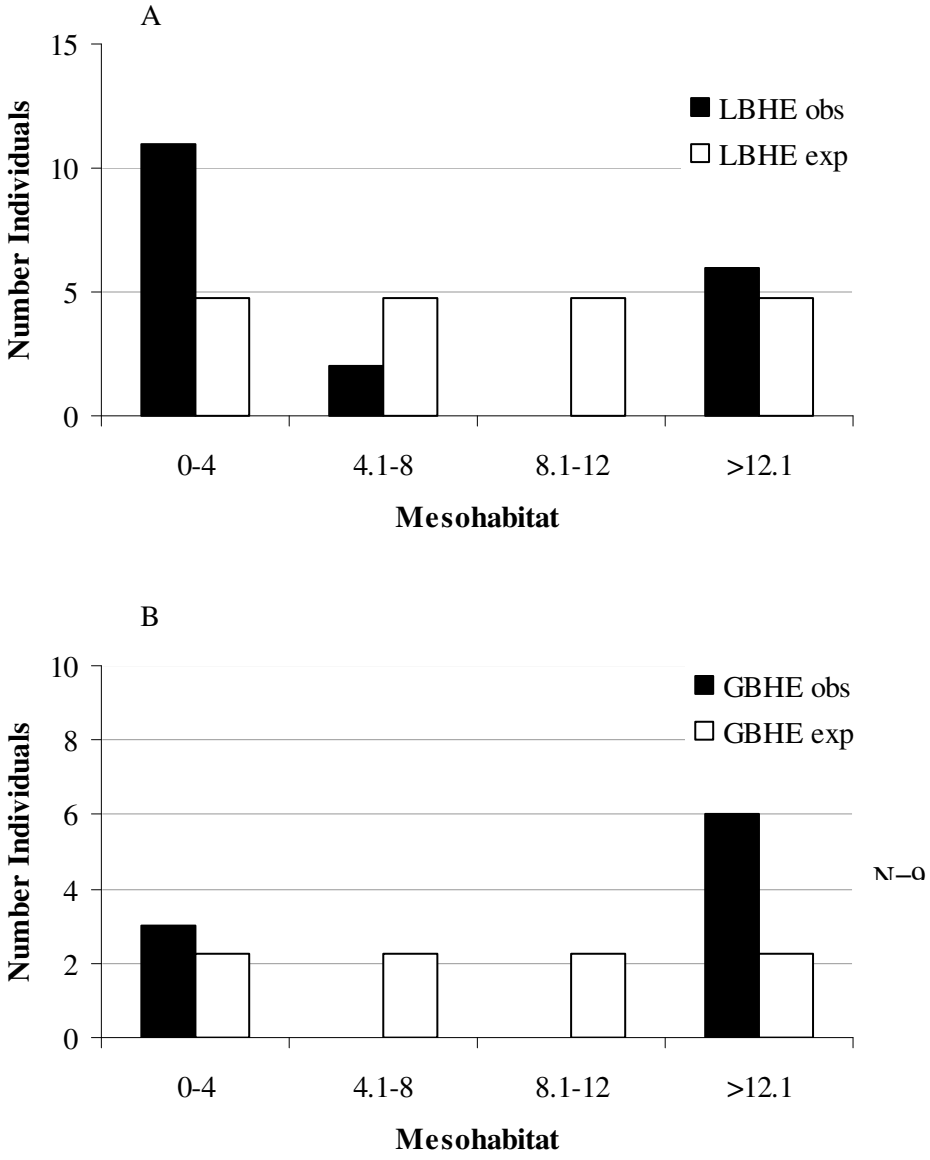

Figure 4.25. A) Patterns of mesohabitat use by Little Blue Herons (*N* = 19) and B) by Great Blue Herons (*N* = 9) at LANWR, Texas during 1998-1999 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

Microhabitat

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Overall, wading birds used water depth both <15 cm and from 16-20 cm more often than expected (*K-S* test, $D = -265.3$, $p < 0.001$) (Fig. 4. 26, Table 4.5). Use of water depth greater than 31 cm was much less than expected. Great Egrets occurred most often in the 16-30 cm water depths and to a lesser extent in the <15 cm ($D = -71.3$, $p < 0.001$), whereas Snowy Egrets showed just the opposite pattern ($D = -102.3$, $p < 0.001$) (Fig.4.27 A, B). Both Tricolored Herons ($D = -15.00$, $p < 0.001$) and Reddish Egrets ($D = -9.6$, $p < .001$) used water depth less than 15 cm more often than expected (Fig. 4.28 A, B). Likewise, White Ibises ($D = -22.6$, $p < 0.001$) and Roseate Spoonbills ($D = -23.6$, $p < 0.001$) also used water depths less than 15 cm more often than expected (Fig. 4. 29 A, B). They also occurred in water depths from 16-30 cm although less often than expected. Little Blue Herons used water depths less than 15 cm. more often than expected ($D = -7.6$, $p < 0.001$) and were also observed in water from 16-30 cm as well as foraging in water greater than 30 cm (Fig 4. 30 A). Great Blue Herons, like other species occurred most often in water less than 15 cm deep ($D = -9.0$, $p < 0.001$) (Fig 4. 30 B). They occurred as expected in water from 16-30 cm and they were not observed in water deeper than 31 cm. Paired comparisons of water depth use between each species showed that Great Blue Herons were utilizing different water depths than all other species except Little Blue Herons (Table 4.6). There was also a significant difference between Great Egrets and Roseate Spoonbills in water depth use.

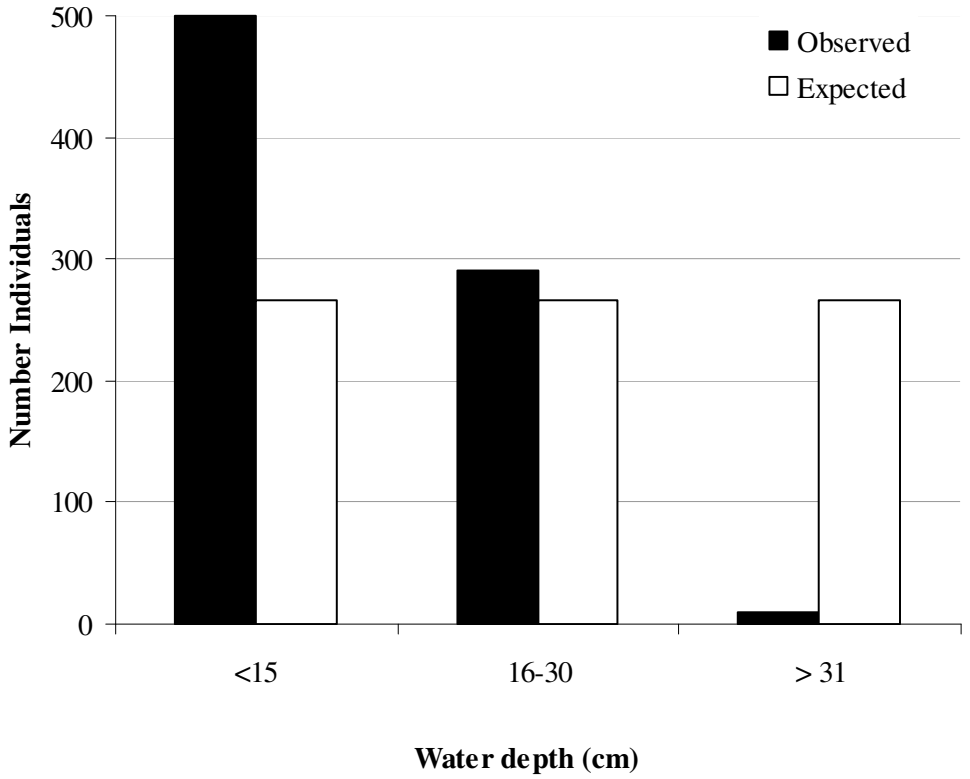

Figure 4.26. Overall wading bird microhabitat (water depth, cm) use at MINWR Tx during 1997-2000 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

Table 4.5. Number of wading bird species observed and expected in different microhabitat categories (water depth cm) in Texas coastal salt marsh MINWR during 1997-2000 fall and winter. Expected frequencies shown here are for Kolmogorov goodness-of-fit tests for each species separately, based on the assumption that all habitat categories were equally accessible.

	Water Depth (cm)			
Species	**<15**	**16–30**	**>31**	***N***
Great Egret	99	111	7	217
Expected	72.3			
Snowy Egret	196	113	1	310
Expected	103.3			
Tricolored Heron	41	7	0	48
Expected	16			
Reddish Egret	28	4	0	10.7
Expected	10.7			
White Ibis	48	23	0	71
Expected	23.7			
Roseate Spoonbill	54	20	0	74
Expected	24.7			
Little Blue Heron	20	5	1	26
Expected	8.7			
Great Blue Heron	14	7	0	21
Expected	7			

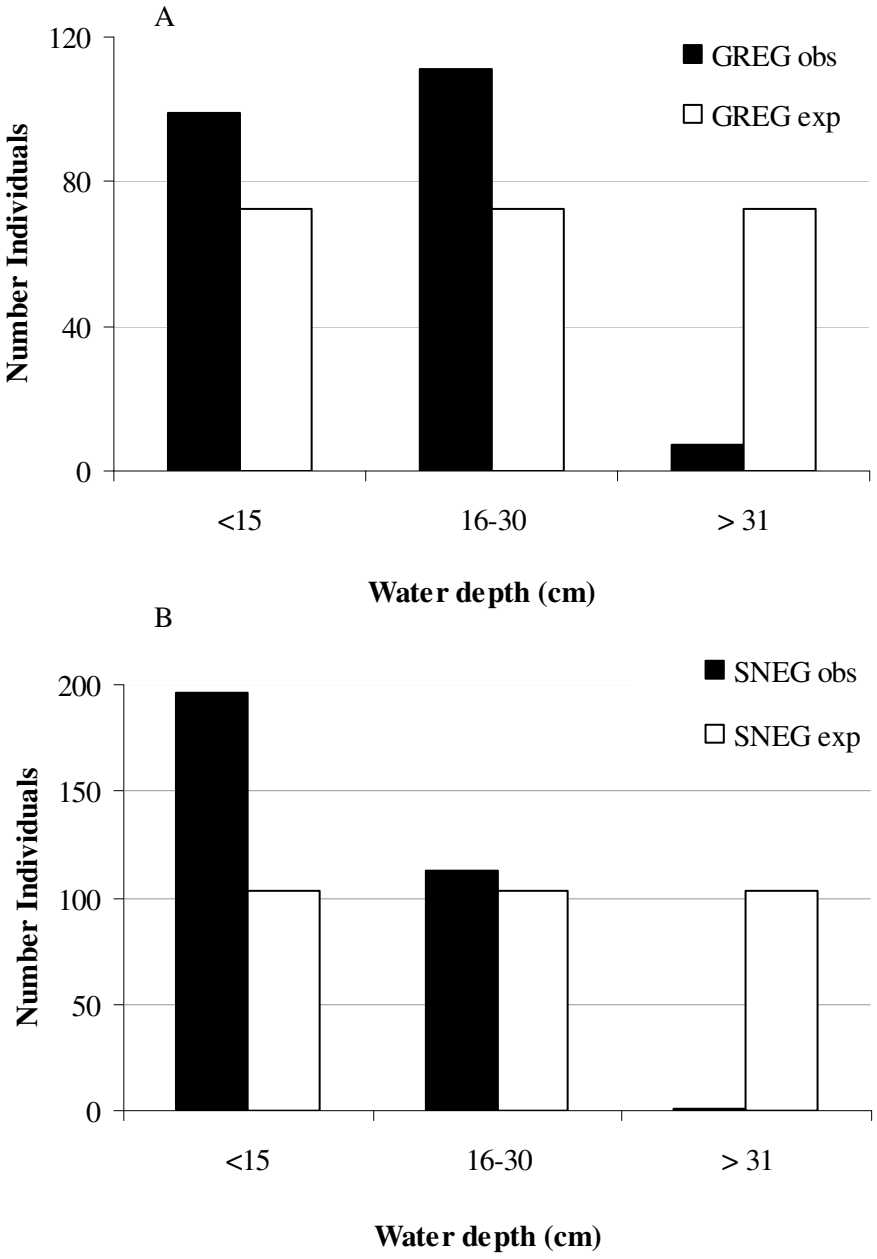

Figure 4.27. A) Patterns of microhabitat use by Great Egrets and B) by Snowy Egrets at MINWR, Texas during 1997-2000 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

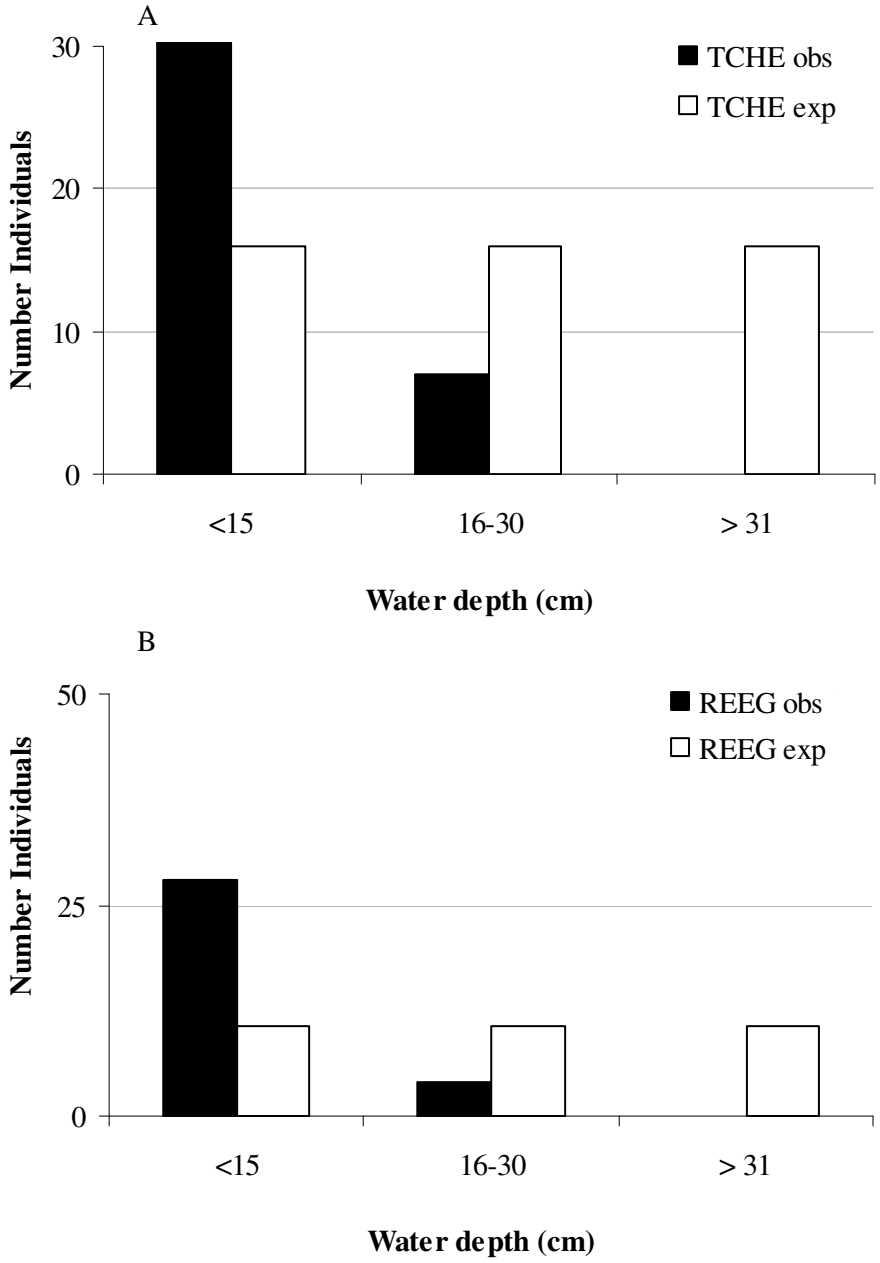

Figure 4.28. A) Patterns of microhabitat use by Tricolored Herons and B) by Reddish Egrets at MINWR, Texas during 1997-2000 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

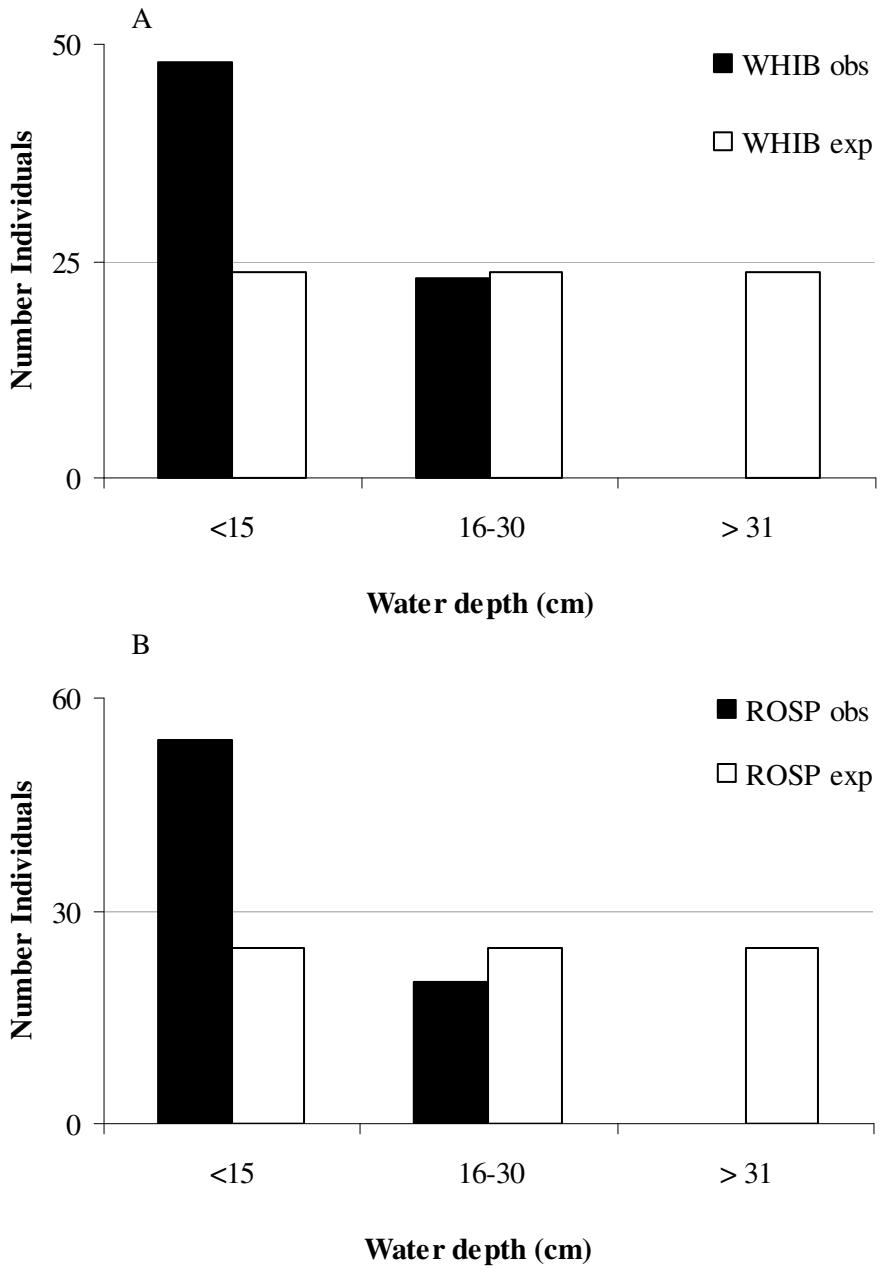

Figure 4.29. A) Patterns of microhabitat use by White Ibises and B) by Roseate Spoonbills at MINWR, Texas during 1997-2000 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

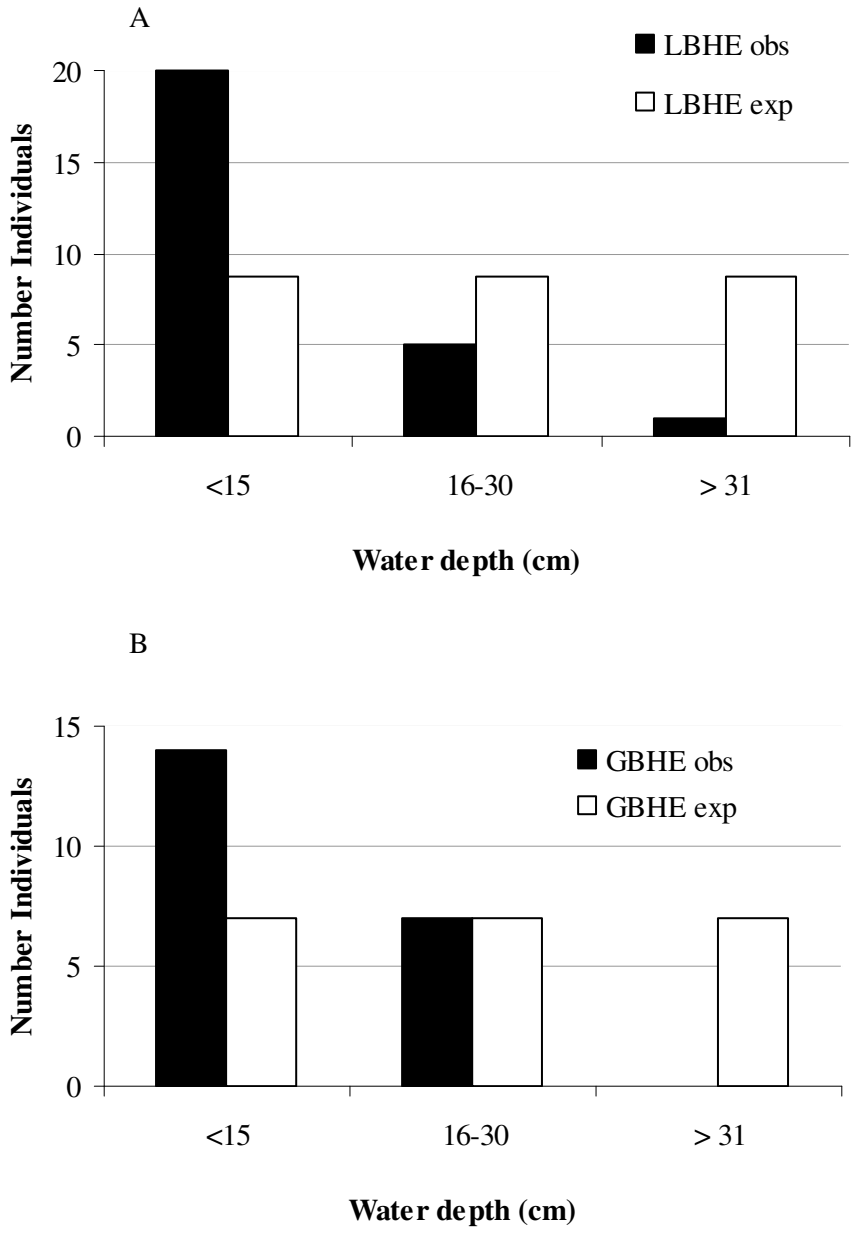

Figure 4.30. A) Patterns of microhabitat use by Little Blue Herons and B) by Great Blue Herons at MINWR, Texas during 1997-2000 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

Table 4.6. Paired comparison between distributions of each species water depth use at Texas coastal marsh, MINWR. Kolmogorov-Smirnov goodness of fit test D values are shown. Species pairs which have significantly different water depth distributions are indicated by an asterisk ($p < .001$).

	GREG	SNEG	TCHE	REEG	WHIB	ROSP	LBHE	GBHE
GREG	x	–0.67	0.33	0.33	0.33	–6.7**	–6.7	–6.0**
SNEG		x	–0.67	0.33	0.33	–0.67	–0.67	–6.33**
TCHE			x	0.33	0.33	0.33	–0.67	–6.33**
REEG				x	0.33	0.33	–0.67	–6.33**
WHIB					x	0.33	–0.67	–6.33**
ROSP						x	–0.67	–6.33**
LBHE							x	–0.33
GBHE								x

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All wading birds at this site also used water depths less than 15 cm more often than expected (*K-S* test, $D = -127.3$, $p < 0.001$) (Fig 4. 31, Table 4.7). There were also more wading birds observed in water depths greater than or equal to 31 cm than at Matagorda Island, although they occurred here less often than expected. Great Egrets were observed more often than expected in water depths greater or equal to 31 cm and from zero to 15 cm ($D = -16.6$, $p < 0.001$) (Fig 4.32 A). Snowy Egrets were observed more often than expected only in water depths from 0-15 cm ($D = -15.2$, $p < 0.001$) (Fig 4. 32 B). Likewise, both Tricolored Herons ($D = -7.6$, $p < 0.001$) (Fig. 4. 33 A) and Reddish Egrets ($D = -6.00$, $p < 0.001$) occurred more often than expected in water depths less than 15 cm (Fig. 4. 33B). White Ibises ($D = -39.3$, $p < 0.001$) (Fig. 4.34 A) and Roseate Spoonbills also (Fig. 4. 34 B)($D = -24.3$, $p < 0.001$) occurred more often than expected in water depths less than 15 cm. Little Blue Herons were observed most often in water depths less than 15 cm (Fig. 4. 35 A) ($D = -3.6$, $p < 0.001$), as were Great Blue Herons (Fig. 4. 35 B) ($D = -9.0$, $p < .001$), however, Great Blue Herons were observed as expected in both 16-30 cm and greater than 31 cm water depths. Paired comparisons of water depth use between each species showed that Great Blue Herons were utilizing different water depths than all other species, except Little Blue Herons (Table 4.8). Great Egrets and Reddish Egrets also had significantly different microhabitat use.

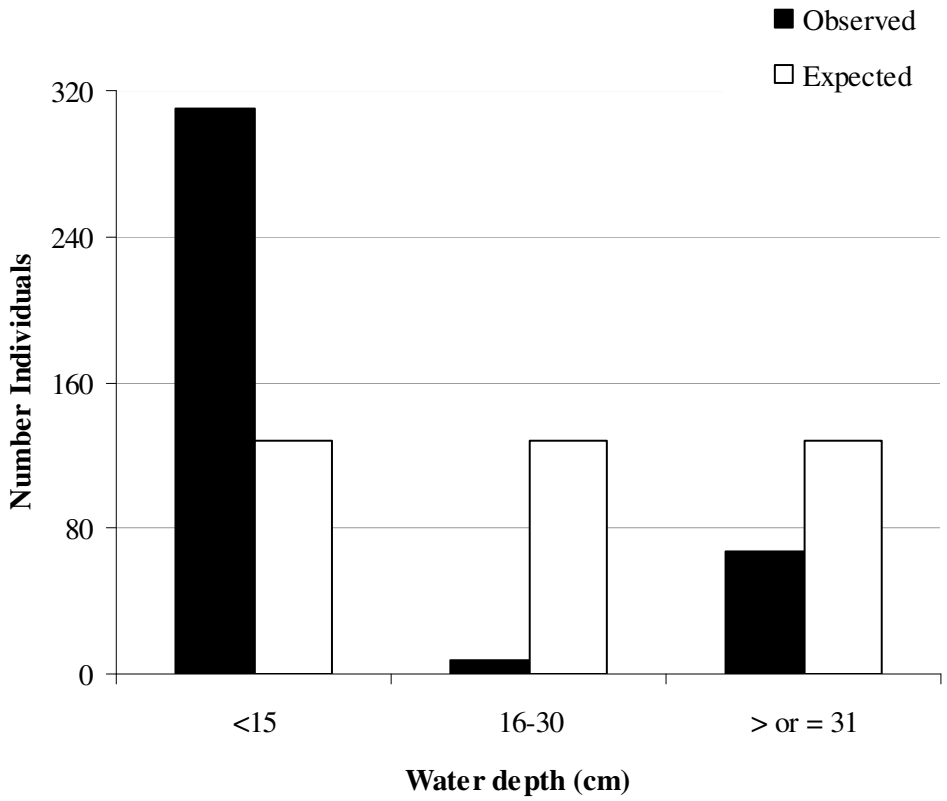

Figure 4.31. Overall wading bird microhabitat (water depth, cm) use at LANWR Tx during 1998-1999 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

Table 4.7. Number of wading bird species observed and expected in different microhabitat categories (water depth cm) in Texas coastal salt marsh LANWR during 1998-1999 fall and winter. Expected frequencies shown here are for Kolmogorov goodness-of-fit tests for each species separately, based on the assumption that all habitat categories were equally accessible.

	Water Depth (cm)			
Species	**<15**	**16–30**	**>31**	***N***
Great Egret	24	3	26	53
Expected	17.7			
Snowy Egret	65	0	2	67
Expected	22.3			
Tricolored Heron	25	0	1	26
Expected	8.7			
Reddish Egret	18	3	0	21
Expected	7			
White Ibis	103	0	18	121
Expected	40.3			
Roseate Spoonbill	62	0	14	76
Expected	25.3			
Little Blue Heron	10	0	4	14
Expected	4.7			
Great Blue Heron	3	2	2	2.3
Expected	2.3			

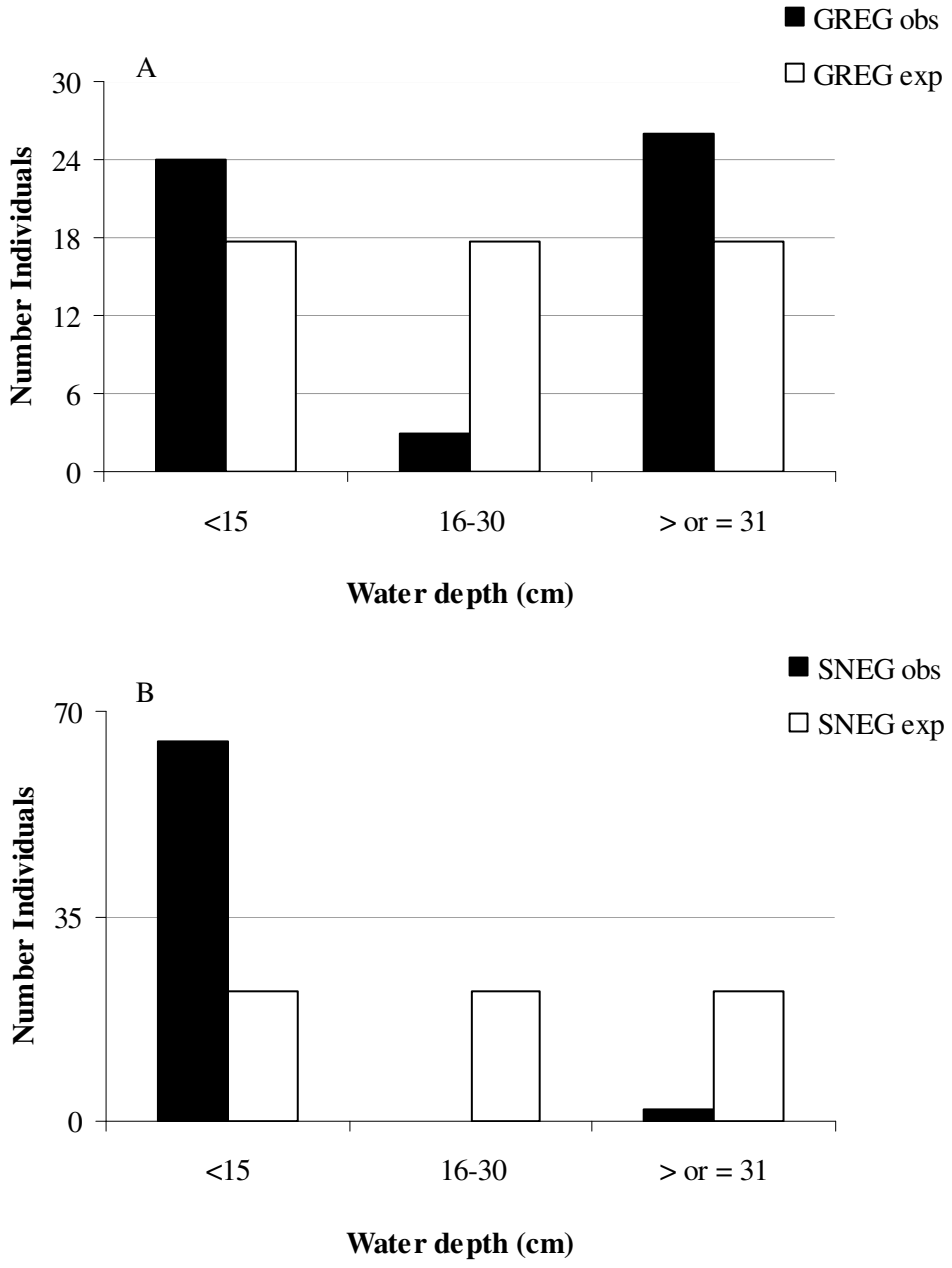

Figure 4.32. A) Patterns of microhabitat use by Great Egrets and B) by Snowy Egrets at LANWR, Texas during 1998-1999 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

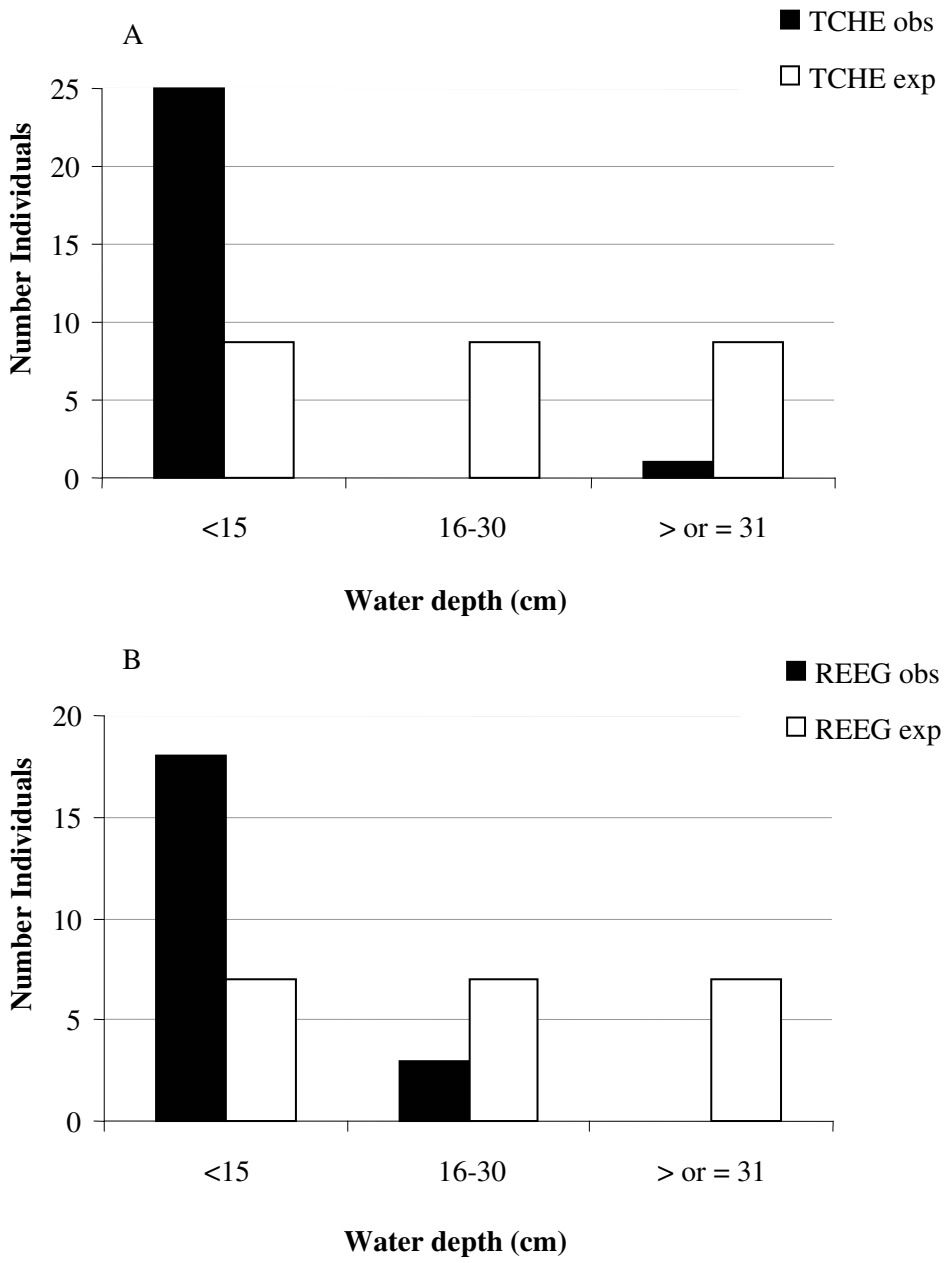

Figure 4.33. A) Patterns of microhabitat use by Tricolored Herons and B) by Reddish Egrets at LANWR, Texas during 1998-1999 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

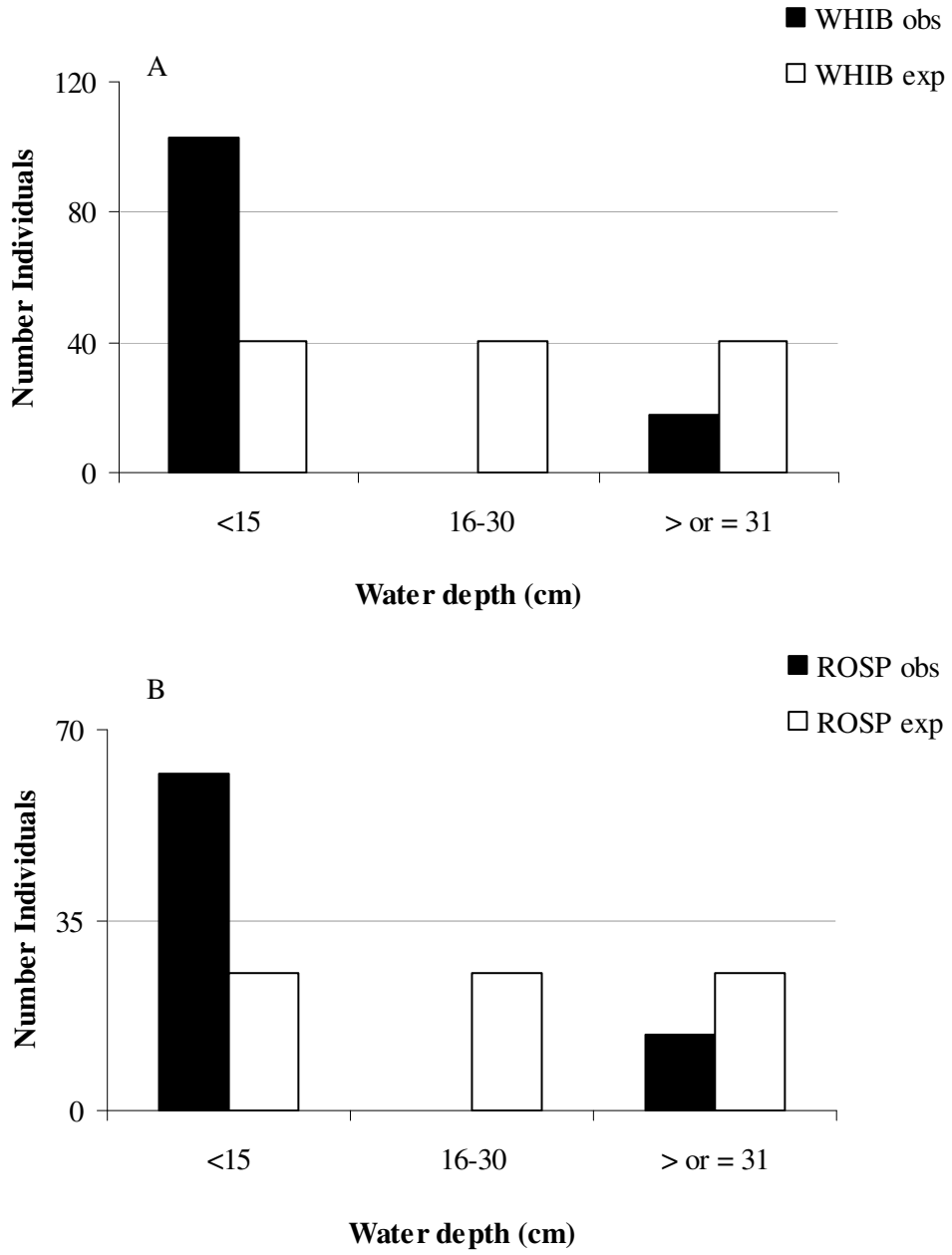

Figure 4.34. A) Patterns of microhabitat use by White Ibises and B) by Roseate Spoonbills at LANWR, Texas during 1998-1999 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

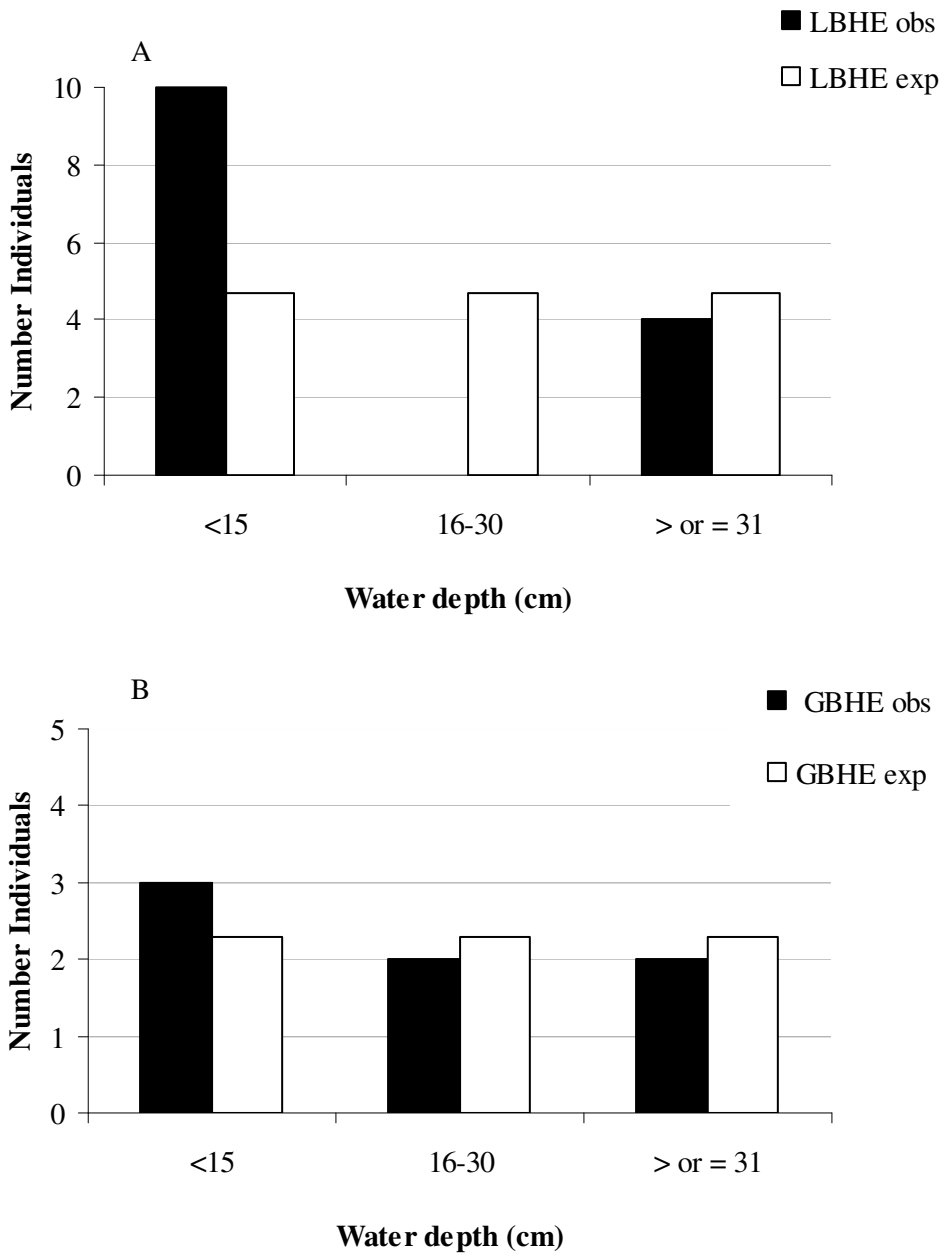

Figure 4.35. A) Patterns of microhabitat use by Little Blue Herons and B) by Great Blue Herons at LANWR, Texas during 1998-1999 fall and winter. White bars represent number of individuals expected and black bars indicate number of individuals observed.

Table 4.8. Paired comparison between distributions of each species water depth use at a Texas coastal marsh, LANWR. Kolmogorov-Smirnov goodness of fit test D values are shown. Species pairs which have significantly different water depth distributions are indicated by an asterisk (* $p<.01$, ** $p<.001$).

	GREG	SNEG	TCHE	REEG	WHIB	ROSP	LBHE	GBHE
GREG	x	0.33	0.33	1*	0.33	0.33	0.33	–1.0*
SNEG		x	0.33	0.67	0.33	0.33	0.33	–1.33**
TCHE			x	0.67	0.33	0.33	0.33	–1.33**
REEG				x	0.67	0.67	0.67	–1.33**
WHIB					x	0.33	0.33	–1.33**
ROSP						x	0.33	–1.33**
LBHE							x	–1.33**
GBHE								x

DISCUSSION

Macrohabitat

I found interspecific differences in macrohabitat use by wintering wading birds at all sites. Overall, wading birds foraging at MINWR occurred in cuts, lakes and vegetated flats, whereas at LANWR species were observed in lagoons, lakes and "channels". Differences in habitat use could be due to several factors including environmental factors (e.g., salinity, water depth), prey characteristics (density, biomass, etc.,) and habitat availability.

Other studies of wading bird habitat use at the macrohabitat level have listed the following factors as being important: size of water body and presence of vegetation (Chavez-Ramirez and Slack 1995); salinity (Ramo and Busto 1993) and water depth (Kushlan 1976a; Custer and Osborn 1978a; Strong *et al.* 1997). At MINWR during the nonbreeding seasons of 1992-93 wading birds were much more likely to use open water habitat than vegetated flats (Chavez-Ramirez and Slack 1995). Similarily, eighty-two percent of all wading birds observed were in an open water habitat versus a vegetated flat. In both studies, high numbers of all wading bird species were observed in lakes, however, I also observed a high number of wading birds in cuts (Table 4.1, Fig. 4.4). Chavez-Ramirez and Slack (1995) also noted high numbers of wading birds in bays, whereas I did not observe this trend (Table 4.1, Fig. 4.4). Perhaps this is due in part to the fact that I used ground surveys rather than aerial surveys and thus had less access to bay areas because of lack of roads.

In areas which have high variation in salinity, researchers have found wading birds partitioning the habitat based on salinity. For example, in the Yucatán, México herons segregated into two groups. The first group included Great Blue Herons, Great Egrets and Snowy Egrets that

used mainly freshwater habitats and the second group was comprised of Reddish Egrets and Tricolored Herons that used saltwater habitats (Ramo and Busto 1993). The only freshwater in my study sites came in the form of precipitation but the lagoons were hypersaline water bodies. All wading bird species at Laguna Atascosa were observed foraging in lagoons, but White Ibises and Roseate Spoonbills occurred in the highest numbers (Table 4.4, Fig. 4.21). In contrast during the breeding season, White Ibis adults are limited to foraging in freshwater sites because chicks cannot process highly saline prey (Bildstein *et al.* 1990). Coastal lagoons could represent important areas for wintering White Ibises at LANWR.

In general, macrohabitat use patterns of individual species did not hold at the regional scale. Wading birds used different habitats at both locations and habitats that were used by the same species in both sites varied in terms of size, presence of vegetation and salinity. When wading bird habitat use was compared across a regional scale in Europe, there was no link between wading bird species and specific habitats (Fasola 1994). Fasola (1994) suggested that wading birds were using the habitat opportunistically based on a combination of factors that were presumably most profitable within each region. Specifically, for large and small wading bird species they found that prey weight and type characterized food resources, whereas species of intermediate size could be characterized by a combination of prey type and foraging habitat.

Species which had high overlap for macrohabitat use in this study tended to use different foraging behaviors. For example, at MINWR four groups emerged. White Ibises and Tricolored Herons comprised the first group and they both shared a preference for vegetated flats (Fig. 4.14). However, White Ibises are primarily tactile foragers, while Tricolored Herons tend to use an active hunting strategy (Willard 1977; Kushlan 1978; Rodgers 1983). A second group included Great Blue Herons, Great Egrets and Reddish Egrets (Fig. 4.14). Great Blue Herons and Great Egrets have similar hunting strategies. Both species prefer slower foraging behaviors such as

"stand and wait" or "slow walking" (Willard 1977; Kushlan 1978). Reddish Egrets are the most active foragers of this group, preferring to use a "disturb and chase" strategy (Rodgers 1983). In other sites, Great Blue Herons and Great Egrets differ most with regard to prey size eaten (Willard 1977; Hom 1983; Ramo and Busto 1993). The third group was comprised of the smaller species, Snowy Egrets and Little Blue Herons (Fig. 4.14). Again, these species forage using different behaviors, with Snowy Egrets being more active hunters than Little Blue Herons (Willard 1977). Roseate Spoonbills had the least overlap with other species (Fig. 4.14).

The results of this study are equivocal regarding Willard's (1977) hypothesis that similar-sized herons overlap in resource use while differently-sized herons differ in their use of similar resources (Jenni 1969; Willard 1977; Custer and Osborn 1978b; Kushlan 1978). At MINWR, this hypothesis seemed to hold true. Generally species of similar sizes (e.g., White Ibises and Tricolored Herons or Great Blue Herons and Great Egrets) tended to have higher overlap in habitat use. At LANWR, the opposite was true. Overlap was highest between species of dissimilar sizes (e.g., Great Egrets and Reddish Egrets, Tricolored Herons and Roseate Spoonbills.

Chavez-Ramirez and Slack (1995) found similar results to those at LANWR, where during the winter, species that were most similar in size showed the least overlap in habitat use patterns (Chavez-Ramirez and Slack 1995). They suggested the difference between their study and others were due to differences between breeding season and nonbreeding season foraging ecology. My results seem to suggest that regional differences in sites also may contribute to differences among results. MINWR is coastal marsh that lacks the lagoons and submergent vegetation that LANWR has. Perhaps landscape differences in habitat availability, as well as differences in prey characteristics among sites contributed to the disparity in these results.

Mesohabitat

At the mesohabitat level all species at MINWR used the edge (0-2 m or 0-4 m) category the most (Table 4.3, Fig. 4.16). This could be due to the shallow nature of this category. Smaller herons, may also stand on vegetation at the edge to forage in water deeper than their leg length. At LANWR, wading birds were observed much farther from the edge. Even smaller species (Snowy Egrets and Little Blue Herons) were seen as far as seventy meters from the edge. Although there was a positive correlation between distance from the edge and water depth, water as far away from the edge as fifty meters was measured at only thirty centimeters. Wading birds have much more foraging habitat available to them here due to the relatively shallow nature of the Gulf of Mexico coast.

Few other studies have examined distance from the edge as a separate habitat component. However, Tricolored Herons in Florida were observed using the edges of deeper water habitats (Jenni 1969). In a salt marsh along southern San Francisco Bay California, Snowy Egrets preferred sites in shallow water close to vegetation and Great Egrets were observed in deeper water close to vegetation suggesting a preference for "edge" habitat (Hom 1983). Great Blue Herons on the other hand, were observed in deep water furthest from vegetation. In Tampa Bay, Florida Great Egrets attained a higher rate of prey capture while hunting along the vegetated shorelines of estuaries (Rodgers 1983) suggesting a benefit to foraging in the "edge" habitat.

At MINWR, Great Egrets, Snowy Egrets, Tricolored Herons, White Ibises, Roseate Spoonbills, Little Blue Herons and Great Blue Herons all used the mesohabitat closest to the edge (e.g., from 0-2 m away from the edge) more often than expected. Reddish Egrets were the only ones to consistently utilize mesohabitat categories further away from the edge. I suspect that this is a result of their active foraging technique, which is considerably different from the "stand and

wait" or "slow wading" foraging techniques used by other wading birds. Running behavior may be used to spot and overtake prey (Kushlan 1978) and use of this behavior to forage may result in Reddish Egrets being drawn away from the edge in pursuit of prey.

At LANWR, all species were observed foraging much farther away from the edge (Table 4.4, Fig. 4.21). This is probably tied to two factors: First, the lagoons in which they were foraging remained shallow enough for wading birds to stand as far away as seventy meters from the edge; and second, submerged vegetation patches located further away from the edge may have contained higher densities of potential prey for wading birds to forage on. Mesohabitat use in these study sites seemed to reflect the shallow nature of the lagoon.

Microhabitat

Water depth has been identified as an important characteristic for wading bird habitat partitioning in other locations (Meyerriecks 1962; Kushlan 1976a; Willard 1977; Custer and Osborn 1978b; Hom 1983; Powell 1987; Dubowy 1996; Dimalexis *et al.* 1997). Studies conducted along the Atlantic coast note the importance of tides (which in turn impact water depth) in affecting wading bird foraging habitat use (Custer and Osborn 1978a, 1978b; Maccarone and Parsons 1994). In the Everglades the seasonal pattern of drying and related changes in water depth were important to wading bird habitat use (Kushlan 1976a 1976; 1978). However, along the Texas shore of the Gulf of Mexico coast, tidal currents are weak (Britton 1989). At these locations strong northerly winds tend to move waters out of tidal inlets and into the Gulf (Britton 1989) and are probably more important in determining availability of wading bird habitat. Additionally, the lagoons at LANWR were relatively shallow hypersaline

waterbodies and as a result of their shallow nature, even smaller wading birds have access to foraging sites throughout the waterbody.

Generally, researchers have found larger foraging wading birds (i.e., longer-legged wading birds) in deeper water than do smaller herons (Meyerriecks 1962; Kushlan 1976a; Custer and Osborn 1978a; Hom 1983). My results are similar in that Great Egrets and Great Blue Herons at both locations were found in all water depth categories, whereas other species were not. Little Blue Herons, the smallest wading bird species, were observed foraging in water depths greater than 31 cm deep and this was accomplished either by standing on the bank and leaning over deeper water, or standing on vegetation to forage in deep water.

In conclusion, I found that wintering wading birds along the Gulf of Mexico coast do seem to be partitioning foraging habitat at all three hierarchical levels. At the macrohabitat level, wintering wading birds showed interspecific differences in habitat use of both open water habitats and vegetated flats. However, patterns of habitat use by individual species did not hold at a regional scale, i.e., species did not seem to be using the same habitat types at all study sites. Macrohabitat overlap tended to be high among species that differed in foraging behavior. I observed regional differences in habitat use at the mesohabitat level. In one location all wading birds were observed foraging near the edge, whereas in the other location wading birds were observed foraging as much as 12 m from the edge most often. I suspect that these differences reflect regional differences in both water depth and presence of vegetation between the sites.

At LANWR most birds were observed foraging in lagoons. The shallow nature of these waterbodies allowed even smaller wading birds to forage farther away from the edge than they could at MINWR. Another important difference between sites was the presence of submerged vegetation or the seagrass beds. Wading birds foraging at LANWR may have been located further away from the edge because they foraged in areas with submerged vegetation, where prey density may be higher. Submerged vegetation may also have allowed shorter-legged wading birds (e.g., Snowy Egrets and Little Blue Herons) to exploit areas where they otherwise would be unable to stand.

Finally, at the microhabitat level, I found that overall wading birds were observed most often in water depths ranging from zero to less than 15 cm. Larger herons (Great Egrets and Great Blue Herons) did tend to utilize water depths that were deeper than other species used, however no clear pattern of habitat partitioning was observed. Interspecific differences in the effects of water depth on foraging wading birds as well as the interaction between water depth and prey availability (e.g., Gawlik 2002) could obscure patterns of microhabitat partitioning.

CHAPTER V

FACTORS AFFECTING FLOCK FEEDING IN MIXED SPECIES ASSEMBLAGES AT MATAGORDA ISLAND NATIONAL WILDLIFE REFUGE, TEXAS

SYNOPSIS

I examined two aspects of wading bird flock foraging during the non-breeding season. I assessed intraspecific differences between wintering wading birds foraging in flocks versus those foraging individually. I hypothesized that birds foraging in flocks should derive more benefits than those foraging individually, thus, they should have reduced step rates, increased strike rates, increased success rates and increased capture efficiency. I also compared interspecific differences between wading birds foraging in flocks versus those foraging individually. I hypothesized that Great Egrets and Snowy Egrets should benefit from flock foraging more than Reddish Egrets, Little Blue Herons and Great Blue Herons. I studied wintering wading bird foraging behavior at Matagorda Island NWR (MINWR), Texas. I drove roads adjacent to marshes and when I encountered a foraging individual or flock I took at least 5 min of video. For each focal individual I collected data for: step rate (steps/min), strike rate (strikes/min), success rate (captures/min), capture efficiency (capture/strike), and whether it was foraging individually or in a flock. I used Chi-square goodness of fit tests to determine if a species foraged in flocks more often than expected by chance. I used Mann-Whitney *U* test to make intraspecific comparisons of behavioral data between flock and solitary feeding wading birds. I compared behavioral data interspecifically among wading birds flock feeding and feeding alone using Kruskal-Wallis tests and compared species pairs using Mann-Whitney *U* tests. Great Egrets (χ^2 =

23.3, $df = 1$, $p < .001$) and Snowy Egrets ($\chi^2 = 20.5$, $df = 1$, $p < .001$) foraged in flocks twice as often as they foraged individually. Intraspecifically, flocking Great Egrets had a higher average strike rate than solitary ones ($z = -2.59$, $p < .01$, $N = 62$) but average capture efficiency of solitary Great Egrets was significantly higher than those in flocks ($z = -2.19$, $p < .01$, $N = 62$). Flocking Snowy Egrets had a significantly lower average strike rate versus those foraging alone ($z = -2.73$, $p < .05$, $N = 47$).

Interspecifically, step rate and strike rate varied significantly among flock feeders. Reddish Egrets and Little Blue Herons had the highest step rates and Great Egrets and Reddish Egrets had the highest strike rate. Success rate of flocking Great Egrets was significantly higher than that of Great Blue Herons or Snowy Egrets. There were also significant differences among solitary foraging species in step rate ($\chi^2 = 26.4$, $df = 5$, $p < .001$, $N = 66$) and strike rate ($\chi^2 = 22.7$, $df = 5$, $p < .001$, $N = 66$). Reddish Egrets had the highest mean step rate and they were significantly different than all other species except for Tricolored Herons. Great Blue Herons had a significantly lower mean step rate ($\bar{X} = 8.5$ steps/min) than all other species. Results indicated that while some species, e.g., Snowy Egrets and Great Egrets benefit from flock foraging, for other species, e.g., Reddish Egrets and Great Blue Herons flock feeding can actually negatively effect various aspects of foraging success to the individual.

INTRODUCTION

Flock feeding is an important aspect of wading bird foraging behavior. During both the breeding and nonbreeding season, wading birds are commonly observed feeding in mixed-species flocks (Kushlan 1976b; Caldwell 1981; Hafner *et al.* 1982; Master 1992; Master *et al.* 1993; Smith 1995). Proposed benefits of mixed-flock feeding for birds can be grouped into two broad

categories: 1) benefits derived during foraging, and 2) anti-predator benefits (reviews in (Morse 1970; Moriarty 1976; Krebs and Davies 1981). Because of the relatively large size of adult wading birds, predation is thought to be a less influential factor in the formation of wading bird feeding flocks than the benefits derived during foraging (Kushlan 1976b; Caldwell 1981). Thus, benefits derived during foraging are probably a more important factor to wading birds.

Not all species, however, benefit equally when foraging in flocks. Factors that may influence actual benefits derived during foraging including variation in plumage color, variation in feeding behaviors and rate of interference or prey-robbing. Species forming the core of foraging flocks (e.g., Snowy Egrets (SNEGs), Great Egrets (GREGs), and Roseate Spoonbills (ROSPs) tend to have lighter-colored plumage than those feeding peripherally e.g., Great Blue Herons (GBHEs), Little Blue Herons (LBHEs), Tricolored Herons (TCHEs), etc. (Kushlan 1978; Master 1992; Master *et al.* 1993). Juvenile LBHEs, which have white plumage, are attacked less often and catch more fish than dark-plumaged adults in mixed species foraging flocks (Caldwell 1981). Light juvenile plumages may have evolved to take advantage of an increase in feeding efficiency while foraging in mixed-species flocks (Caldwell 1981).

Species-specific foraging behaviors may negatively affect foraging success in a flock. Species that utilize highly active foraging behavior, e.g., Reddish Egrets (REEGs) have increased agonistic interactions when foraging in a flock (Kushlan 1978). Likewise, species that methodically search may capture fewer prey while foraging in a flock due to disturbance created by other more active species (Kushlan 1978). Species at the core of feeding aggregations tend to feed either by standing, e.g., SNEGs or GREGs (Caldwell 1980; 1981; Master 1992; Master *et al.* 1993) or by slow tactile feeding, as in ROSPs or White Ibises (WHIBs) rather than by using highly active foraging behavior (e.g., disturb-and-chase) such as REEGs do (Kushlan 1978).

Additional costs associated with flock foraging include interference and other negative social interactions, such as prey robbing (kleptoparasitism). Prey robbing has been reported in several species of wading birds and it can occur both within and among species (Kushlan 1978; Amat and Rilla 1994).

The majority of work that has been done on foraging wading birds has been done during the breeding season, while the non-breeding season has received little attention. Factors that could influence feeding during the non-breeding season include changes in prey movements due to changing temperatures in tidal marshes, less restrictive diets for adults because they are no longer feeding chicks and the influx of migrant birds to coastal marshes. The objective of this research was to assess intraspecific differences among wintering wading birds foraging in flocks versus those foraging individually. I hypothesized that during the nonbreeding season, as in the breeding season, individual birds foraging in flocks would derive more benefits than those foraging individually. I measured benefits in behavioral terms of step rate, strike rate, success rate and capture efficiency. The predictions were that birds that benefit from foraging in flocks should lead to reduced step rates, increased strike rates, increased success rates and increased capture efficiency.

The second component of the research was to compare interspecific differences among birds foraging in flocks versus those foraging individually. The hypothesis was that lighter colored species should benefit from flock foraging more than darker colored species i.e., Great Egrets and Snowy Egrets will derive greater benefits from flock foraging than Reddish Egrets, Little Blue Herons and Great Blue Herons. Species such as Great Egrets and Snowy Egrets, which tend to form the core of mixed species aggregations tend to feed visually or by slow non-visual feeding (e.g., White Ibis). Whereas, other species, e.g., Great Blue Herons, Reddish

Egrets, etc. are forced by lowered foraging efficiency to feed at the periphery of or away from an aggregation (Kushlan 1976b).

METHODS

I studied wintering wading bird foraging behavior at Matagorda Island NWR (MINWR), located in the coastal bend region of Texas, Calhoun County (Fig. 5.1). The refuge is a barrier island, 62 km long that varies from 1.2 to 7.3 km wide. The salt marsh areas were located on the west side of the island and consisted of vegetated flats dominated by glasswort, saltwort, sea-oxeye daisy, wolfberry, saltgrass, smooth cordgrass, and wind tidal flats dominated by mudflat grass, saltgrass and cordgrasses.

I located wading birds by driving roads adjacent to marshes at least once a month for a minimum of three consecutive days from 6 October 1997 through 28 March 1998; from 5 October 1998 through 23 March 1999; and from 16 October 1999 through 19 March 2000. All surveys were conducted from a truck along roads adjacent to the marshes. When a foraging individual or flock (herein defined as two or more individuals less than or equal to 5 meters apart) was encountered, a minimum of 5 min of video was taken. I used a Canon 8 mm video camcorder to record wading bird foraging behavior.

During playback of videotapes, all individuals that could be observed for the full 5 min were selected and were observed for 5 min periods for a total of two hundred and four 5 min units. I collected the following data for each focal individual: step rate (steps/min), strike rate (strikes/min), success rate (captures/min), capture efficiency (capture/strike), and whether bird was foraging individually or in a flock.

I used Chi-square goodness of fit tests to determine if species foraged in flocks more often than expected by chance. To examine overall behavioral differences between birds foraging in flocks versus individually, I grouped all species of wading birds into two categories, those foraging in aggregations and those foraging individually, and compared behavioral variables between these two groups using Mann-Whitney *U* tests. To compare behavioral variables intraspecifically between all birds foraging in flocks versus those foraging individually, I also used Mann-Whitney *U* tests because the data did not meet the assumptions necessary for t-tests. Finally to compare interspecific differences in foraging behavior, I divided the data into two groups, wading birds foraging in aggregations and those foraging individually, I then compared behavioral variables among species within each category using a Kruskal-Wallis test. Individual pairs of species were compared using Mann-Whitney *U* tests to determine which species pairs were significantly different with regard to foraging behaviors.

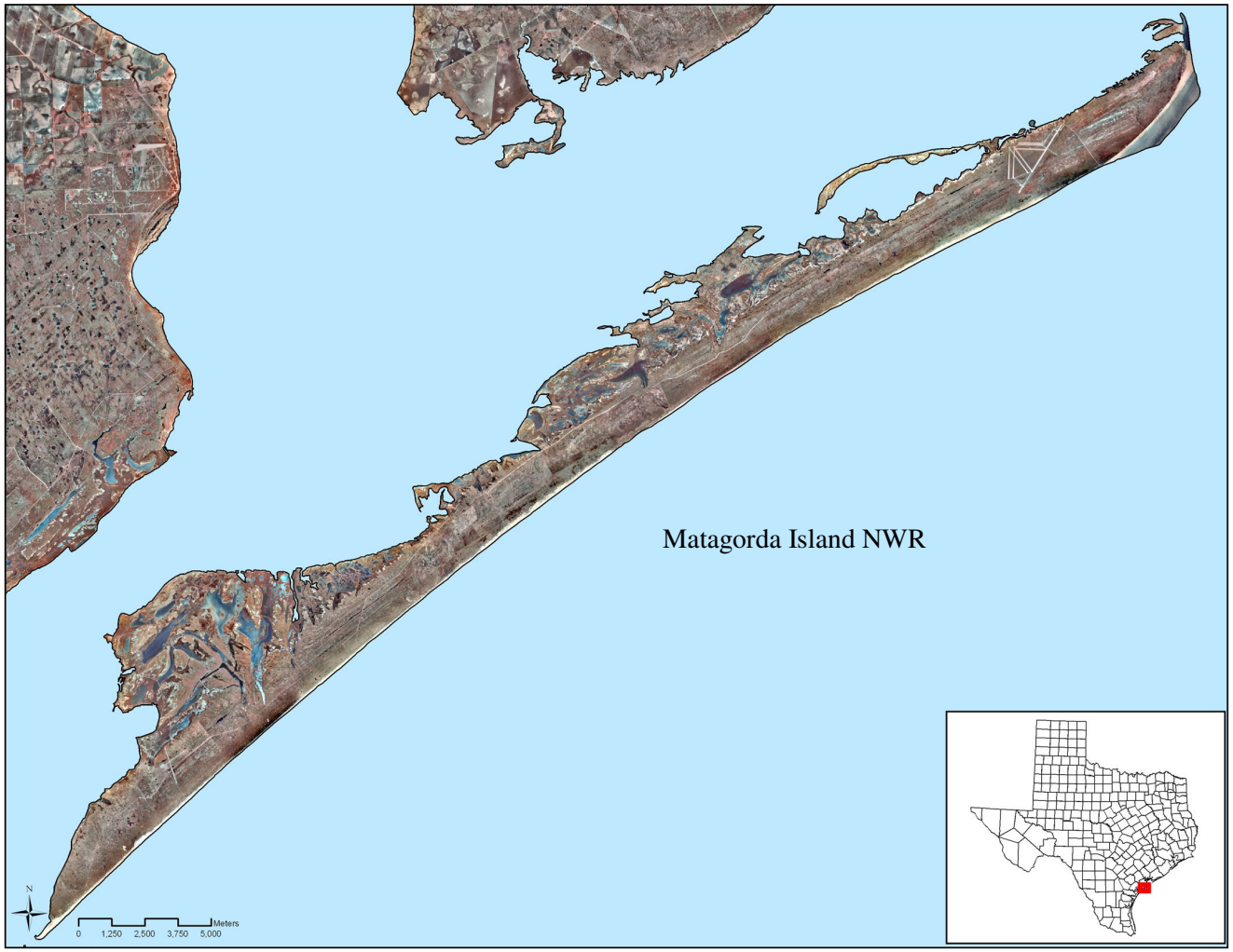

Figure 5.1. Matagorda Island NWR, Texas.

RESULTS

I observed the following species of wading birds foraging individually: Great Egrets (N = 12), Snowy Egrets (N = 8), Reddish Egrets (N = 20), Tricolored Herons (N = 9), Little Blue Herons (N = 9) and Great Blue Herons (N = 7). I observed the following species of wading birds foraging in flocks: Great Egrets (N = 50), Snowy Egrets (N = 39), Reddish Egrets (N = 10), Tricolored Herons (N = 6), Little Blue Herons (N = 8) and Great Blue Herons (N = 9).

Flock Participation

There were interspecific differences in flock participation. Light colored species foraged in flocks more often than expected. Great Egrets (χ^2 = 23.3, df = 1, p<.001) and Snowy Egrets (χ^2 = 20.5, df = 1, p<.001) foraged in flocks twice as often as they foraged individually (Fig 5.2). Great Blue Herons (χ^2 = 0.25, df = 1, p > .05), Little Blue Herons (χ^2 = 0.06, df = 1, p > .05), Tricolored Herons (χ^2 = 0.6, df = 1, p > .05) and Reddish Egrets (χ^2 = 3.33, df = 1, p > .05) were equally likely to forage alone or in flocks (Fig. 5.3).

When I combined all species and compared behavioral variables between wading birds foraging in flocks and those foraging individually, I found that birds that foraged alone had a significantly greater step rate than those foraging in aggregations (z = –3.184, p <.001, N = 187) (Fig. 5.4). There were no significant differences in capture efficiency (z = –1.7, p = .09, N = 187) (Fig 5.5), strike rate (z = –0.84, p > .05, N = 187) (Fig. 5.6) or success rate (z = –1.5, p > .05, N = 187) (Fig. 5.7) between birds foraging in flocks or those foraging alone when all species were combined.

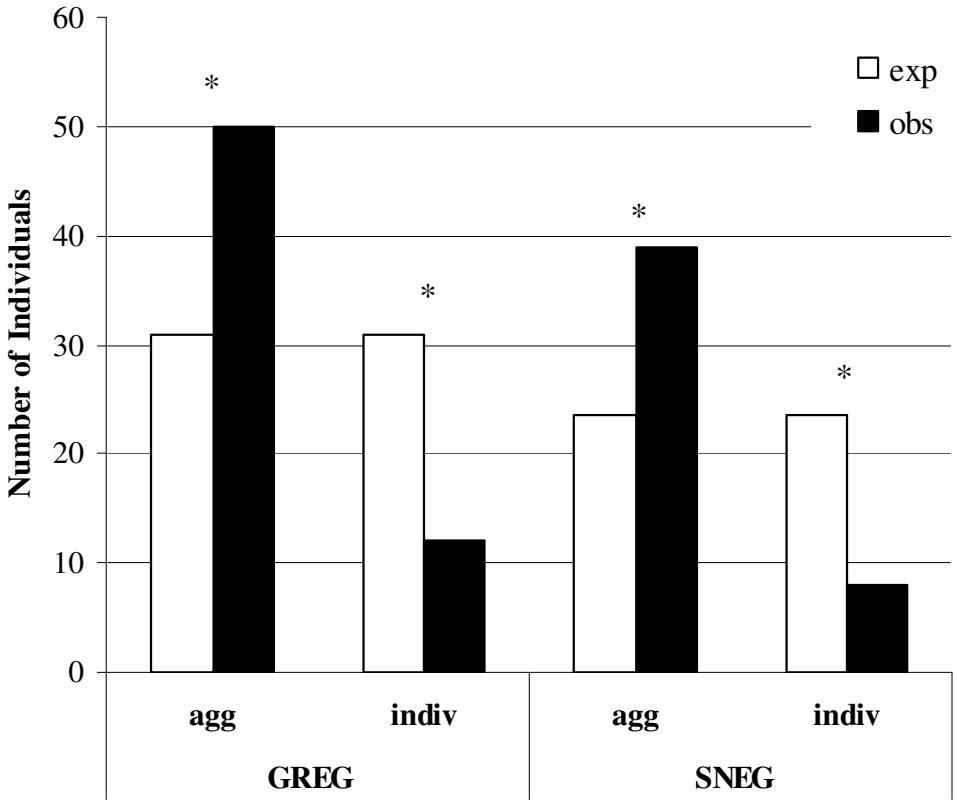

Figure 5.2. Flock participation by Great Egrets and Snowy Egrets at MINWR. White bars represent number of individuals expected and black bars indicate number of individuals observed. * indicates significant differences.

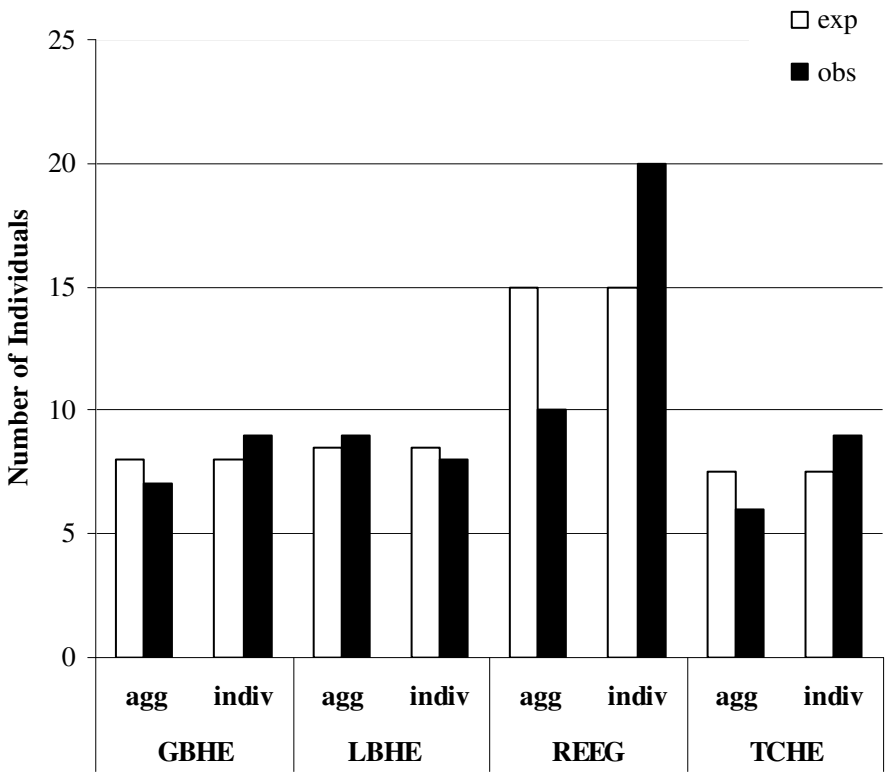

Figure 5.3. Flock participation by Great Blue Herons, Little Blue Herons, Reddish Egrets and Tricolored Herons at MINWR. White bars represent number of individuals expected and black bars indicate number of individuals observed. * indicates significant differences.

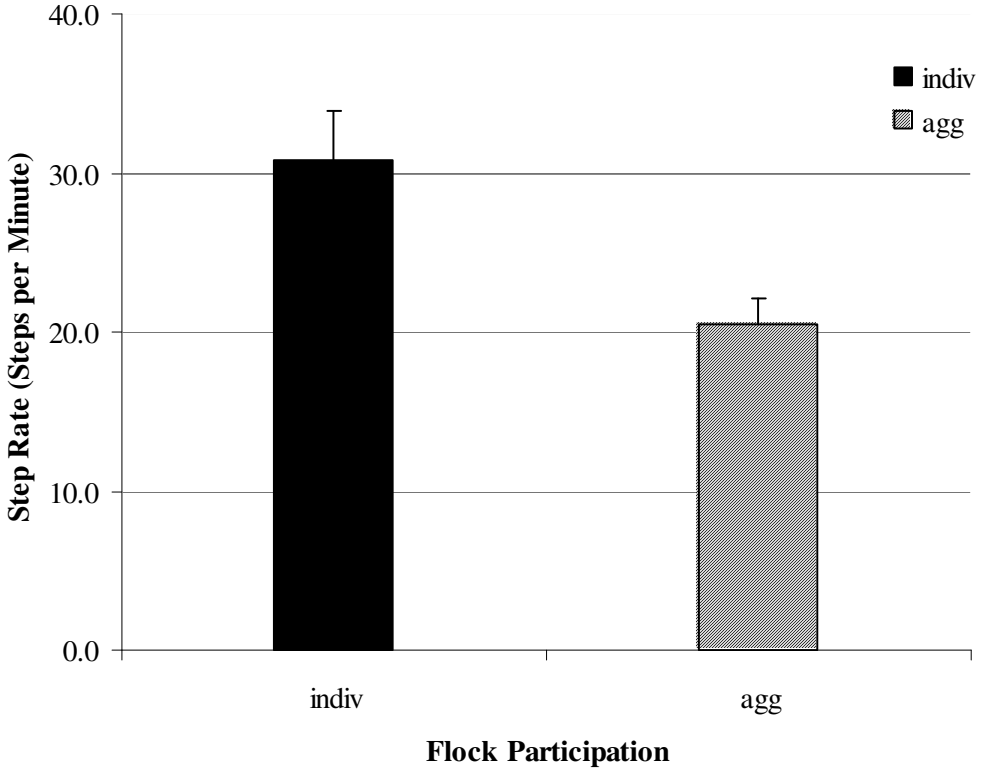

Figure 5.4. Overall comparison of step rate between wading birds foraging individually (*N* = 66) or in an aggregation (*N* = 121) using Mann-Whitney *U* test (*= *p* <.05). Black bars indicate birds foraging individually. Striped bars indicate birds foraging in aggregations.

*

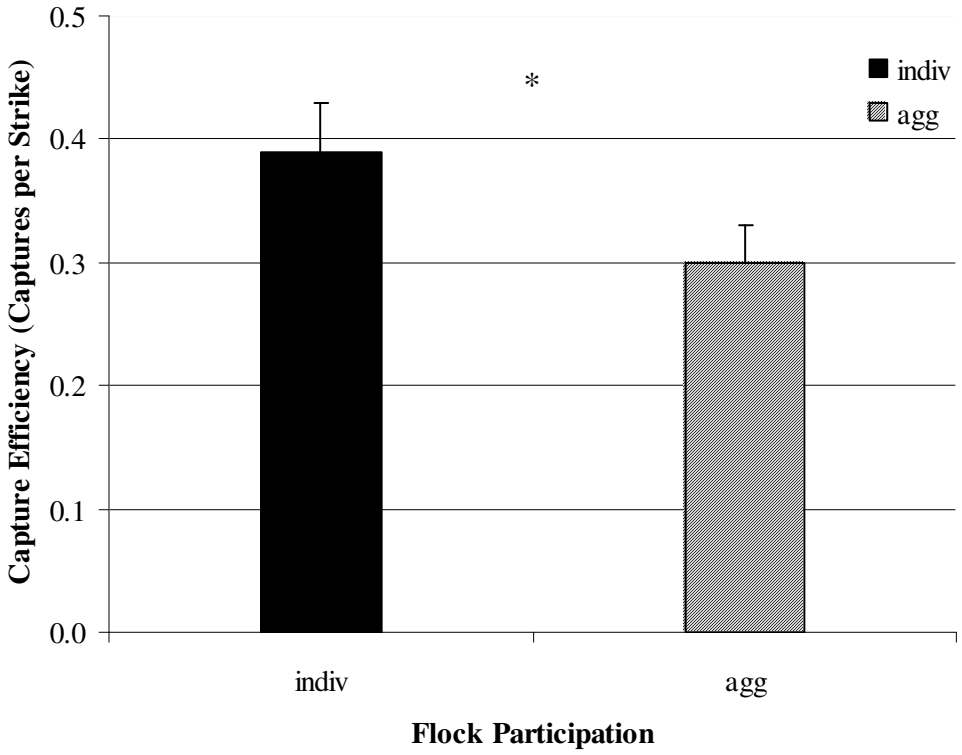

Figure 5.5. Overall comparison of capture efficiency between wading birds foraging individually (*N* = 66) or in an aggregation (*N* = 121) using Mann-Whitney *U* test (*=*p* < .05). Black bars indicate birds foraging individually. Striped bars indicate birds foraging in aggregations.

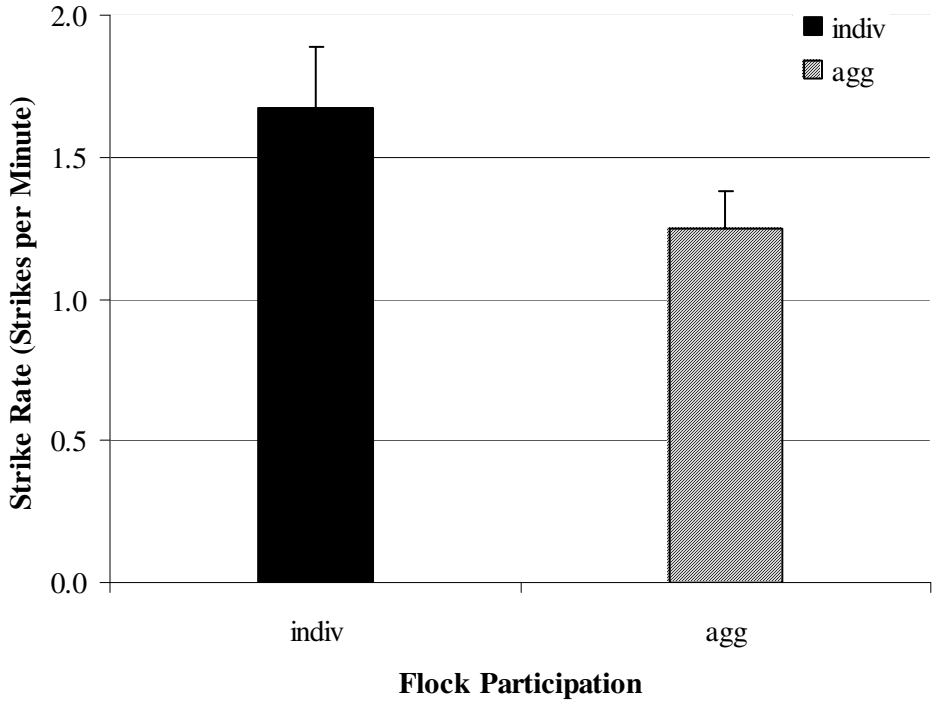

Figure 5.6. Overall comparison of strike rate between wading birds foraging individually (*N* = 66) or in an aggregation (*N* = 121) using Mann-Whitney *U* test ($p > .05$). Black bars indicate birds foraging individually. Striped bars indicate birds foraging in aggregations.

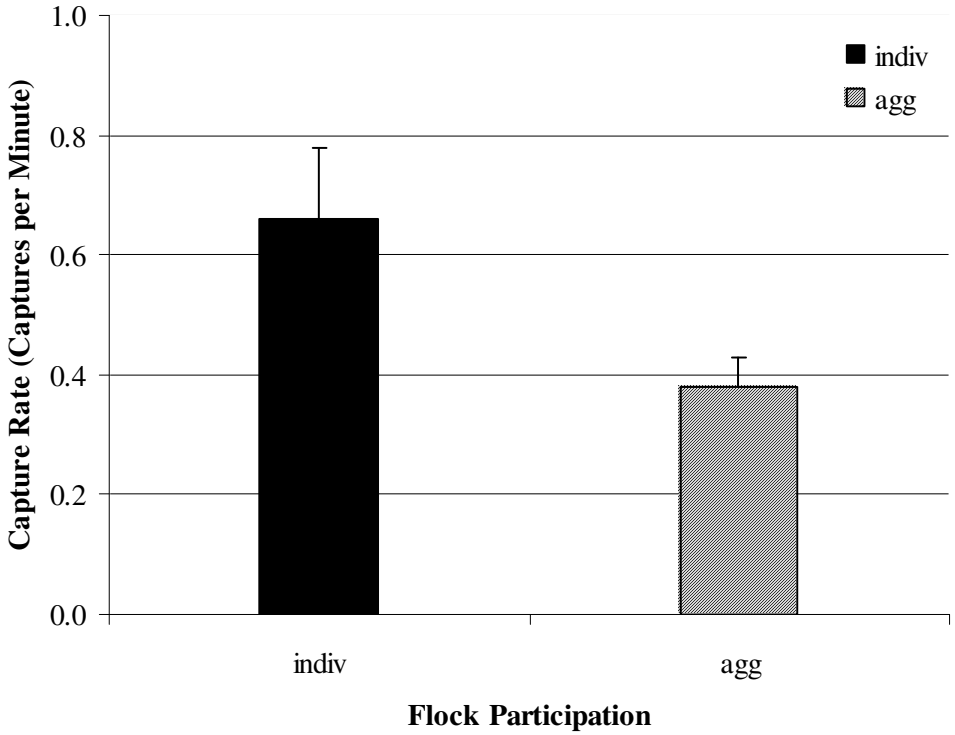

Figure 5.7. Overall comparison of success rate between wading birds foraging individually (*N* = 66) or in an aggregation (*N* = 121) using Mann-Whitney *U* test (*p* > .05). Black bars indicate birds foraging individually. Striped bars indicate birds foraging in aggregations.

Intraspecific Differences

When I compared behavioral variables for birds foraging in flocks versus individually within a species, Great Egrets and Snowy Egrets were the only species in which there were significant differences (Table 5.1). Great Egrets foraging in flocks had a higher average strike rate than when foraging alone ($z = –2.59$, $p < .01$, $N = 62$). However, the average capture efficiency of Great Egrets foraging alone was significantly higher than the capture efficiency of those birds foraging in flocks ($z = –2.19$, $p < .01$, $N = 62$). Snowy Egrets foraging in flocks had a significantly lower average strike rate versus those foraging alone ($z = –2.73$, $p < .05$, $N = 47$). There was no difference in success rate between Snowy Egrets foraging individuals versus those foraging in flocks ($z = –1.93$, $p = .05$, $N = 62$). There were no significant differences in behavioral variables between birds foraging in flocks versus those foraging alone for any of the other species (Great Blue Herons, Tricolored Herons, Little Blue Herons and Reddish Egrets) (Table 5.1).

Table 5.1. Intraspecific comparisons of foraging rates between wading birds foraging in aggregations and individually at MINWR during 1997-2000 fall and winter.

Foraging Rate	**Flock***	***N***	**Mean**	***SE***	***Z***	***P***
Great Egret						
Step Rate	indiv	12	12.28	2.17	–.009	n.s.
(steps/min)	agg	50	12.74	1.28		
Strike Rate	indiv	12	058	0.16	–2.59	<.01
(strikes/min)	agg	50	1.57	0.24		
Success rate	indiv	12	030	0.05	–.220	n.s.
(captures/min)	agg	50	0.50	0.10		
Capture Efficiency	indiv	12	0.58	0.11	–2.19	<.01
(captures/strike)	agg	50	0.31	0.04		
Snowy Egret						
Step Rate	indiv	8	29.55	9.11	–1.00	n.s.
(steps/min)	agg	39	19.05	2.32		
Strike Rate	indiv	8	2.45	0.68	–2.73	<.05
(strikes/min)	agg	39	0.88	0.16		
Success rate	indiv	8	0.93	0.44	–1.93	.05
(captures/min)	agg	39	0.25	0.05		
Capture Efficiency	indiv	8	0.30	0.10	–0.66	n.s.
(captures/strike)	agg	39	0.27	0.05		
Great Blue Heron						
Step Rate	indiv	10	8.56	3.28	–0.868	n.s.
(steps/min)	agg	6	4.83	1.85		
Strike Rate	indiv	10	0.24	0.08	–1.03	n.s.
(strikes/min)	agg	6	0.40	0.13		
Success rate	indiv	10	0.12	0.04	–0.365	n.s.
(captures/min)	agg	6	0.13	0.10		
Capture Efficiency	indiv	10	0.39	0.15	–0.543	n.s.
(captures/strike)	agg	6	0.29	0.19		

Table 5.1(cont'd)

Foraging Rate	**Flock***	***N***	**Mean**	***SE***	***Z***	***P***
Tricolored Heron						
Step Rate	indiv	9	34.62	7.25	–1.18	n.s.
(steps/min)	agg	6	18.10	7.42		
Strike Rate	indiv	9	1.91	0.44	–1.30	n.s.
(strikes/min)	agg	6	1.07	0.64		
Success rate	indiv	9	0.69	0.24	–0.96	n.s.
(captures/min)	agg	6	0.33	0.16		
Capture Efficiency	indiv	9	0.34	0.11	–0.18	n.s.
(captures/strike)	agg	6	0.33	0.15		
Reddish Egret						
Step Rate	indiv	21	49.02	6.17	–1.29	n.s.
(steps/min)	agg	9	32.40	8.80		
Strike Rate	indiv	21	2.35	0.44	–0.70	n.s.
(strikes/min)	agg	9	1.87	0.62		
Success rate	indiv	21	0.71	0.21	–0.14	n.s.
(captures/min)	agg	9	0.62	0.22		
Capture Efficiency	indiv	21	0.28	0.05	–0.41	n.s.
(captures/strike)	agg	9	0.34	0.11		
Little Blue Heron						
Step Rate	indiv	8	26.88	4.18	–0.36	n.s.
(steps/min)	agg	9	31.02	4.44		
Strike Rate	indiv	8	2.05	0.77	–0.19	n.s.
(strikes/min)	agg	9	1.20	0.28		
Success rate	indiv	8	1.38	0.55	–0.78	n.s.
(captures/min)	agg	9	0.33	0.09		
Capture Efficiency	indiv	8	0.53	0.13	–0.83	n.s.
(captures/strike)	agg	9	0.36	0.13		

*indiv = individually; agg = aggregation

Interspecific Comparisons Among Flocking Birds

There were significant differences in step rate among species foraging in flocks (KW, χ^2 = 22.19, *df* = 5, $p < .001$, *N* = 121) and strike rate (χ^2 = 12.07, *df* = 5, $p < .05$, *N* = 121) (Table 5.2). There were no significant differences among species for success rate or capture efficiency when all species were grouped together (Table 5.2).

Reddish Egrets and Little Blue Herons had the highest step rates among birds foraging in flocks, and they both had significantly higher step rates than Great Egrets and Great Blue Herons (Table 5.3). There were no significant differences in step rate among Little Blue Herons, Reddish Egrets and Tricolored Herons. Little Blue Herons foraging in flocks had a significantly higher step rate than Snowy Egrets; however, there was no significant difference between Reddish Egrets and Snowy Egrets. Great Blue Herons had the lowest step rate and they were significantly different than all other species except for Tricolored Herons. Likewise, Great Egrets also had a relatively low step rate, which was significantly different from all species except for Snowy Egrets and Tricolored Herons.

Great Egrets and Reddish Egrets had the highest strike rate among wading birds foraging in flocks (Table 5.4). The strike rate of Great Egrets foraging in flocks was significantly higher than either Great Blue Herons or Snowy Egrets foraging in flocks. No other species pairs were significantly different in strike rate.

The success rate of Great Egrets foraging in flocks was significantly higher than that of Great Blue Herons or Snowy Egrets. No other species pairs differed significantly in their success rate while foraging in flocks (Table 5.5). All species had similar capture efficiencies ranging from Snowy Egrets ($\bar{X}$ = 0.27) to Little Blue Herons ($\bar{X}$ = 0.36). There were no significant differences among species pairs (Table 5.6).

Table 5.2. Summary of statistical comparisons of foraging behavior variables among species for wading birds foraging in flocks at MINWR during 1997-2000 fall and winter. Mean foraging behavior and standard error are shown for each species. Kruskal-Wallis tests were used to compare behavioral data among species. *=$p < .05$, **=$p < .001$.

Foraging behavior	***N***	$\overline{X}$	***SE***	X^2	***df***	***p***
Step rate (steps/min)				22.19	5	**
Great Egret	50	12.74	1.28			
Great Blue Heron	7	5.20	1.61			
Snowy Egret	39	19.05	2.32			
Little Blue Heron	9	31.02	4.44			
Tricolored Heron	5	18.1	7.42			
Reddish Egret	10	30.3	8.1			
Strike Rate (strikes/min)				12.07	5	*
Great Egret	50	1.57	0.24			
Great Blue Heron	7	0.46	0.12			
Snowy Egret	39	0.88	0.16			
Little Blue Heron	9	1.2	0.28			
Tricolored Heron	5	1.07	0.64			
Reddish Egret	10	1.78	0.57			
Success Rate (captures/min)				8.11	5	n.s.
Great Egret	50	0.50	0.10			
Great Blue Heron	7	0.14	0.08			
Snowy Egret	39	0.25	0.05			
Little Blue Heron	9	0.33	0.26			
Tricolored Heron	5	0.33	0.16			
Reddish Egret	10	0.58	0.20			
Capture Efficiency (captures/strike)				2.77	5	n.s.
Great Egret	50	0.31	0.04			
Great Blue Heron	7	0.29	0.16			
Snowy Egret	39	0.27	0.05			
Little Blue Heron	9	0.36	0.13			
Tricolored Heron	5	0.33	0.15			
Reddish Egret	10	0.32	0.10			

* $p < .05$
**$p < .001$

Table 5.3. Comparison of step rate (steps/min) between wading bird species pairs foraging in flocks during 1997-2000 fall and winter at MINWR, Texas. Statistical differences (Mann-Whitney *U* tests) between species are indicated:*$p < .05$, **$p < .01$, ***$p < .001$, n.s., not significant.

Species pair	*Z*	*p*
Great Egret–Great Blue Heron	–2.15	*
Great Egret–Snowy Egret	–1.96	0.05
Great Egret–Reddish Egret	–1.99	*
Great Egret–Little Blue Heron	–3.54	***
Great Egret–Tricolored Heron	–0.33	n.s.
Great Blue Heron–Snowy Egret	–2.91	**
Great Blue Heron–Reddish Egret	–2.49	*
Great Blue Heron–Little Blue Heron	–3.12	**
Great Blue Heron–Tricolored Heron	–1.57	n.s.
Snowy Egret–Reddish Egret	–1.09	n.s.
Snowy Egret–Little Blue Heron	–2.36	**
Snowy Egret–Tricolored Heron	–0.47	n.s.
Reddish Egret–Little Blue Heron	–0.20	n.s.
Reddish Egret–Tricolored Heron	–1.19	n.s.
Tricolored Heron–Little Blue Heron	–1.77	n.s.

Table 5.4. Comparison of strike rate (strikes/min) between wading bird species pairs foraging in flocks during 1997-2000 fall and winter at MINWR, Texas. Statistical differences (Mann-Whitney *U* tests) between species are indicated:*$p < .05$, **$p < .01$, ***$p < .001$, n.s., not significant.

Species pair	*Z*	*p*
Great Egret–Great Blue Heron	–2.55	*
Great Egret–Snowy Egret	–2.60	**
Great Egret–Reddish Egret	0.00	n.s.
Great Egret–Little Blue Heron	–0.18	n.s.
Great Egret–Tricolored Heron	–1.34	n.s.
Great Blue Heron–Snowy Egret	–1.00	n.s.
Great Blue Heron–Reddish Egret	–1.77	n.s.
Great Blue Heron–Little Blue Heron	–1.81	n.s.
Great Blue Heron–Tricolored Heron	0.00	n.s.
Snowy Egret–Reddish Egret	–1.42	n.s.
Snowy Egret–Little Blue Heron	–1.33	n.s.
Snowy Egret–Tricolored Heron	–0.42	n.s.
Reddish Egret–Little Blue Heron	–0.41	n.s.
Reddish Egret–Tricolored Heron	–1.20	n.s.
Tricolored Heron–Little Blue Heron	–0.89	n.s.

Table 5.5. Comparison of success rate between wading bird species pairs foraging in flocks during 1997-2000 fall and winter at MINWR, Texas. Statistical differences (Mann-Whitney *U* tests) between species are indicated:*$p < .05$, **$p < .01$, ***$p < .001$, n.s., not significant.

Species pair	*Z*	*p*
Great Egret–Great Blue Heron	–2.01	*
Great Egret–Snowy Egret	–2.13	*
Great Egret–Reddish Egret	–0.14	n.s.
Great Egret–Little Blue Heron	–0.11	n.s.
Great Egret–Tricolored Heron	–0.58	n.s.
Great Blue Heron–Snowy Egret	–0.86	n.s.
Great Blue Heron–Reddish Egret	–1.69	n.s.
Great Blue Heron–Little Blue Heron	–1.54	n.s.
Great Blue Heron–Tricolored Heron	–0.99	n.s.
Snowy Egret–Reddish Egret	–1.47	n.s.
Snowy Egret–Little Blue Heron	–1.13	n.s.
Snowy Egret–Tricolored Heron	–0.49	n.s.
Reddish Egret–Little Blue Heron	–0.29	n.s.
Reddish Egret–Tricolored Heron	–0.73	n.s.
Tricolored Heron–Little Blue Heron	–0.30	n.s.

Table 5.6. Comparison of mean capture efficiency (captures/strike) between wading bird species pairs foraging in flocks during 1997-2000 fall and winter at MINWR, Texas. Statistical differences (Mann-Whitney *U* tests) between species are indicated:*$p < .05$, **$p < .01$, ***$p < .001$, n.s., not significant.

Species pair	*Z*	*p*
Great Egret–Great Blue Heron	–0.91	n.s.
Great Egret–Snowy Egret	–1.42	n.s.
Great Egret–Reddish Egret	–0.12	n.s.
Great Egret–Little Blue Heron	–0.02	n.s.
Great Egret–Tricolored Heron	–0.15	n.s.
Great Blue Heron–Snowy Egret	–0.29	n.s.
Great Blue Heron–Reddish Egret	–0.75	n.s.
Great Blue Heron–Little Blue Heron	–0.82	n.s.
Great Blue Heron–Tricolored Heron	–0.60	n.s.
Snowy Egret–Reddish Egret	–0.87	n.s.
Snowy Egret–Little Blue Heron	–0.78	n.s.
Snowy Egret–Tricolored Heron	–0.54	n.s.
Reddish Egret–Little Blue Heron	–0.17	n.s.
Reddish Egret–Tricolored Heron	0.00	n.s.
Tricolored Heron–Little Blue Heron	0.00	n.s.

Interspecific Comparisons among Solitary Birds

There were also significant differences among species foraging alone for step rate (χ^2 = 26.4, *df* = 5, $p < .001$, *N* = 66) and strike rate (χ^2 = 22.7, *df* = 5, $p < .001$, *N* = 66 (Table 5.7). Neither success rate (χ^2 = 8.5, *df* = 5, n.s., *N* = 66) nor capture efficiency (χ^2 = 5/8, *df* = 5, n.s., *N* = 66) was significantly different among species (Table 5.7).

When I compared step rate among species pairs, I found several groups emerged. Reddish Egrets had the highest mean step rate ($\bar{X}$ = 49.0 steps/min) and they were significantly different than all other species except for Tricolored Herons ($\bar{X}$ = 34.6 steps/min) (Table 5.8). Great Blue Herons had a significantly lower mean step rate ($\bar{X}$ = 8.5 steps/min) than all other species (Table 5.8). Great Egrets ($\bar{X}$ = 12.2 steps/min) had a significantly lower mean step rate than Reddish Egrets, Tricolored Herons and Little Blue Herons but they did not differ significantly from Snowy Egrets (Table 5.8). Little Blue Herons, Snowy Egrets and Tricolored Herons all had an intermediate mean step rate and they did not differ significantly from each other (Table 5.8).

Snowy Egrets, Reddish Egrets, Tricolored Herons and Little Blue Herons all had similar strike rates and did not differ significantly from each other (Table 5.8). Great Blue Herons had the lowest strike rate ($\bar{X}$ = 0.2 strikes/min). Great Egrets had a significantly lower strike rate ($\bar{X}$ = 0.6 strikes/min) than all other species except for Great Blue Herons and Little Blue Herons (Table 5.8).

Table 5.7. Comparisons of foraging behavior variables among species for wading birds foraging individually at MINWR during 1997-2000 fall and winter. Mean foraging behavior and standard error are shown for each species. Kruskal-Wallis tests were used to compare behavioral data among species. *=$p < .05$, **=$p < .001$.

Foraging behavior	***N***	$\overline{X}$	***SE***	X^2	***df***	***p***
Step rate (steps/min)				26.43	5	**
Great Egret	12	12.2	2.2			
Great Blue Heron	9	8.5	3.2			
Snowy Egret	8	29.6	9.1			
Little Blue Heron	8	26.9	4.2			
Tricolored Heron	9	34.6	7.3			
Reddish Egret	20	49	6.2			
Strike Rate (strikes/min)				22.73	5	**
Great Egret	12	0.6	0.16			
Great Blue Heron	9	0.24	0.08			
Snowy Egret	8	2.5	0.68			
Little Blue Heron	8	2.1	0.77			
Tricolored Heron	9	1.9	0.44			
Reddish Egret	20	2.4	0.44			
Success Rate (captures/min)				8.55	5	ns
Great Egret	12	0.3	0.05			
Great Blue Heron	9	0.12	0.04			
Snowy Egret	8	0.93	0.44			
Little Blue Heron	8	1.4	0.56			
Tricolored Heron	9	0.7	0.24			
Reddish Egret	20	0.71	0.21			
Capture Efficiency (captures/strike)				5.82	5	ns
Great Egret	12	1.6	0.4			
Great Blue Heron	9	0.85	0.4			
Snowy Egret	8	2.8	1.1			
Little Blue Heron	8	1.1	0.26			
Tricolored Heron	9	3.0	1.0			
Reddish Egret	20	4.1	0.8			

* $p < .05$
**$p < .001$

Table 5.8. Comparison of step rate (steps/min) among wading bird species pairs foraging individually during 1997-2000 fall and winter at MINWR, Texas. Statistical differences (Mann-Whitney *U* tests) between species are indicated:*$p < .05$, **$p < .01$, ***$p < .001$, n.s., not significant.

Species pair	*Z*	*p*
Great Egret–Great Blue Heron	–1.99	*
Great Egret–Snowy Egret	–1.61	n.s.
Great Egret–Reddish Egret	–3.58	***
Great Egret–Little Blue Heron	–2.62	**
Great Egret–Tricolored Heron	–2.27	**
Great Blue Heron–Snowy Egret	–2.02	*
Great Blue Heron–Reddish Egret	–3.47	**
Great Blue Heron–Little Blue Heron	–2.50	*
Great Blue Heron–Tricolored Heron	–2.60	**
Snowy Egret–Reddish Egret	–1.98	*
Snowy Egret–Little Blue Heron	–0.11	n.s.
Snowy Egret–Tricolored Heron	–0.67	n.s.
Reddish Egret–Little Blue Heron	–2.34	*
Reddish Egret–Tricolored Heron	–1.74	n.s.
Tricolored Heron–Little Blue Heron	–0.87	n.s.

Table 5.9. Comparison of strike rate (strikes/min) between wading bird species pairs foraging individually during 1997-2000 fall and winter at MINWR, Texas. Statistical differences (Mann-Whitney *U* tests) between species are indicated:*$p < .05$, **$p < .01$, ***$p < .001$, n.s., not significant.

Species pair	*Z*	*p*
Great Egret–Great Blue Heron	–2.08	*
Great Egret–Snowy Egret	–2.72	**
Great Egret–Reddish Egret	–2.92	**
Great Egret–Little Blue Heron	–1.09	n.s.
Great Egret–Tricolored Heron	–2.40	*
Great Blue Heron–Snowy Egret	–3.21	**
Great Blue Heron–Reddish Egret	–3.80	***
Great Blue Heron–Little Blue Heron	–2.28	*
Great Blue Heron–Tricolored Heron	–2.87	**
Snowy Egret–Reddish Egret	–0.15	n.s.
Snowy Egret–Little Blue Heron	–0.74	n.s.
Snowy Egret–Tricolored Heron	–0.43	n.s.
Reddish Egret–Little Blue Heron	–0.54	n.s.
Reddish Egret–Tricolored Heron	–0.36	n.s.
Tricolored Heron–Little Blue Heron	–0.15	n.s.

DISCUSSION

Flock feeding is an important component of wading bird behavior and wading birds often feed in large mixed-species flocks. Benefits of flock feeding fall into two categories: avoidance of predation and benefits derived during foraging (Morse 1970; Krebs 1974; Moriarty 1976). Although predation may become a more important factor to wading birds in the temperate and subtropical zones due to the recovery of the Bald Eagle (Butler and Vennesland 2000), currently it is thought to be a less important factor driving flock formation in wading birds.

Wading birds can benefit from feeding in a flock in several ways. Birds that forage in flocks decrease search time between food patches, increase likelihood of foraging in beneficial locations, decrease risk of obtaining no food and increase energy consumption (Kushlan 1978). If the first three factors are more important in driving flock formation, then I predict that birds in flocks experience no increase in energy expenditure but benefit by finding high quality food patches, having a decreased risk of not finding food and a shorter search time between food patches. I will refer to this as the "food-guarantee hypothesis". Species that fall into "food-guarantee hypothesis" category would show no difference in behavioral measures (step rate, strike rate, success rate or capture efficiency) whether foraging in flocks or alone. Conversely, if an increase in energy consumption is driving flock formation then I predict that those birds feeding in flocks should have decreased number of steps and strikes and increased success rate or capture efficiency when in flocks. I will call this the "increased energy hypothesis". There are two ways a heron can increase its number of captures per minute: one is to increase the proportion of successful strikes (i.e., capture efficiency); or, with the same success rate, increase the total number of strikes taken.

Along the Texas Gulf coast during the nonbreeding season, I found that Great Egrets and Snowy Egrets, both light-colored species, participated more often in flock foraging and derived more benefits from feeding in flocks than other species. Great Egrets feeding in flocks had a higher mean strike rate than those foraging alone, whereas, Snowy Egrets had a higher success rate foraging in flocks than those foraging alone. In the case of Snowy Egrets and Great Egrets, my results support the "increased energy hypothesis" i.e., both species benefited by foraging in flocks. Great Egrets and Snowy Egrets are known to be "attractors" of other species to feeding areas (Armstrong 1971; Kushlan 1977; Caldwell 1981; Bildstein *et al.* 1990; Master 1992; Bildstein *et al.* 1994; Gawlik 2002). Gawlik (2002) showed that lighter colored species (e.g., Snowy Egrets, White Ibis and Wood Storks) selected high quality patches. Thus, it behooves lighter colored species to feed more efficiently in flocks, because more often than not, they find themselves foraging in flocks. This pattern has been demonstrated in different locations and at different times of the year. For example, Snowy Egrets in salt marshes of New Jersey during the breeding season had a higher mean capture rate and capture efficiency when foraging in flocks than alone (Master 1992). Likewise, Little Egrets in the Camargue, southern France found that birds feeding in flocks always had significantly better success rate than single birds (Hafner *et al.* 1982). During the breeding season in Texas, Great Egrets feeding in groups had higher strike rates, capture rates and capture success than those feeding alone (Wiggins 1991).

In the case of the darker-colored species (e.g., Great Blue Herons, Little Blue Herons, Tricolored Herons and Reddish Egrets) my results supported the "food-guarantee hypothesis". These species either showed no difference in behaviors between birds foraging in flocks versus those foraging alone or they actually did worse when they foraged in flocks. This pattern has held in other locations as well. When the foraging behavior of adult Little Blue Herons was compared to that of immature Little Blue Herons (which are white), adult Little Blue Herons

caught significantly fewer fish per unit time than did immature birds (Recher and Recher 1969). Squacco Herons (a darker species) had a lower percentage of successful captures than Little Egrets (light-colored species) when foraging in flocks. Solitary Squacco Herons obtained more food per min than those foraging in flocks (Hafner *et al.* 1982).

Although foraging in flocks may not have directly benefited darker species, they may have decreased search time between food patches, increased the likelihood of foraging in beneficial locations, decreased the risk of obtaining no food and increased energy consumption (Kushlan 1978). For these species, finding prey is the challenge. Great Blue Herons, Tricolored Herons, Little Blue Herons and Reddish Egrets may have learned to exploit the superior eyesight of Snowy Egrets (Caldwell 1979) in their search for quality food patches. In Florida, Snowy Egrets were among the wading bird species found to be an "honest" indicator of high quality food patches (Gawlik 2002). In conclusion, my results indicate that while some species, e.g., Snowy Egrets and Great Egrets benefit from flock foraging, for other species, e.g., Reddish Egrets and Great Blue Herons flock feeding is actually detrimental to the individual. However, these species may offset this cost by decreasing their time searching for food. In habitats such as coastal marshes, where prey is located in concentrated patches the cost of locating food may be greater for some species than the ability to maximize energy gain when flock foraging. Future research with banded birds should include between species comparisons of time spent searching for food to determine if darker species spend more time searching for food than lighter species.

CHAPTER VI

CONCLUSIONS

The concept of niche pervades ecological studies. As such, it has been defined in various ways. Grinnell was the first to coin the term. He viewed the niche as the functional role and position of an organism in its community. As the definition of the niche evolved, it also became more quantitative, leading to Hutchinson's formal definition of the niche: an *n*-dimensional hypervolume enclosing the complete range of conditions under which the organism can successfully replace itself. This can be depicted graphically by plotting numerous resource axes that depict the range of environmental conditions necessary for survival and reproduction of an organism.

As ecological niches have been defined for specific organisms, other studies have sought to determine niche overlap, wherein two or more organisms use the same resources or environmental variables, and processes that influence niche overlap, such as competition. With their large size, their tendency to feed in large flocks and their high visibility, wading birds are an excellent group with which to examine questions of niche overlap.

I studied the composition, distribution and foraging ecology of wintering wading birds along the Gulf of Mexico coast. I focused on the geographic variability in wintering wading bird assemblages, the processes that structured these assemblages and habitat use by wading birds. I found considerable variation among three sites spanning the Gulf of Mexico, Aransas National Wildlife Refuge (ANWR), Texas; Marsh Island Wildlife Refuge (MIWR), Louisiana; and Chassahowitzka National Wildlife Refuge (CNWR), Florida. When I compared wintering wading bird assemblages across three regions of the Gulf of Mexico coast several patterns

emerged. First, species comprising wintering wading bird assemblages varied regionally. ANWR, Texas had the most species rich assemblage, with eight different wading bird species including, Great Egrets, White Ibis, Snowy Egrets, Roseate Spoonbills, Great Blue Herons, Tricolored Herons, Reddish Egrets, and Little Blue Herons. MIWR, Louisiana had only six wading bird species. And CNWR, Florida only had three different species, Great Egrets, White Ibis and Great Blue Herons.

The processes that structured wintering wading bird assemblages also varied regionally. In ANWR, Texas, the Random Fraction niche apportionment model (RF model) best explained the empirical abundance data for ANWR. This implies that resources were not limited in ANWR and there was high niche overlap between invading species and existing species in regards to resource use (e.g., food type and/or habitat type). Although I did not examine overlap in food type, I did determine overlap in habitat use within each region. At ANWR, of the seven wading bird species that I determined open-water-habitat overlap, six of the seven had habitat overlap indices of 0.90 or higher (Little Blue Herons were excluded due to small sample sizes).

For abundance data from MIWR a good fit was obtained with the MacArthur Fraction (MF) model and the Power Fraction model (PF) models. These two models are similar in that they both predict that as new species invade a niche, they are more likely to invade either the largest niches or to affect those species with the highest abundances. The most abundant species I saw at MIWR was Snowy Egrets, followed closely by Roseate Spoonbills and Great Egrets. Interestingly, Snowy Egrets had the lowest overlap in habitat use with the other species, preferring to use smaller bodies of water than the other species.

None of the models fully explained the CNWR abundance data. There were sampling difficulties here in that flights had to be conducted at twice the altitude in this location compared to other locations. As a result I recorded only three species, Great Egrets, White Ibis and Great

Blue Heron here. Ground surveys indicated that at least one other species, Little Blue Herons, were present at this location, however they were not detected on flights. Perhaps other processes not accounted for in the model are structuring wintering wading bird assemblages here. Among these three species, open-water habitat overlap was much lower than in other locations. Habitat may have been an important factor in niche partitioning in this location.

I also examined patterns of habitat partitioning among wintering wading birds at three different scales (macro, meso and microhabitat scales) at two sites on the Texas coast, Matagorda Island National Wildlife Refuge (MINWR) and Laguna Atascosa National Wildlife Refuge (LANWR). I found that wintering wading birds partitioned foraging habitat at all three hierarchical levels. At the macrohabitat level, wintering wading birds showed interspecific differences in macrohabitat use of both open water habitats and vegetated flats. However, patterns of macrohabitat use varied among study sites. At MINWR wading birds foraged in cuts, lakes and vegetated flats, whereas at LANWR they foraged primarily in lagoons, lakes and "channels" (a category that included both inlets and cuts). Species which had high overlap in macrohabitat-use patterns used different foraging behaviors. At the mesohabitat level all species at MINWR used the category nearest the edge (land-water interface) most often. At LANWR I observed wading birds most often in the mesohabitat category of 8.1-12 m. from the edge. This reflected differences in water depth as one moved away from the edge of a waterbody. The lagoons at LANWR were much more shallow than the lakes or cuts at MINWR. At MINWR wading birds used water depth both <15 cm and from 16-20 cm more often than expected. All wading birds at LANWR also used water depths less than 15 cm more often than expected. Great Egrets and Great Blue Herons at both locations were found in all water depth categories, whereas other species were not.

Wading birds partition habitat based on water depth. At ANWR, water depth is significantly influenced by wind direction, which in turn, is dependent on winter weather patterns. Perhaps the relatively random nature of the water depth has led to an assemblage where there is high niche overlap and no one species can gain a strong competitive advantage. I predict that in areas where water depth is tied more closely to cyclical processes (e.g., tidally driven), wading bird assemblages would be more then likely be structured by competition. Resources (in this case, available foraging sites) would be more restrictive and wading bird assemblages would show stronger evidence of competition in their composition.

In the final aspect of this research, I found that Great Egrets and Snowy Egrets, both light-colored species, participated more often in flock foraging and derived more benefits from feeding in flocks than other species. Great Egrets feeding in flocks had a higher mean strike rate than those foraging alone, whereas Snowy Egrets had a higher success rate foraging in flocks than those foraging alone. In the case of these species, my results support the "increased energy hypothesis". Both Great Egrets and Snowy Egrets tend to feed more often in flocks and thus benefit from flock foraging. In the case of the darker-colored species (e.g., Great Blue Herons, Little Blue Herons, Tricolored Herons and Reddish Egrets) my results supported the "food-guarantee hypothesis". These species either showed no difference in behaviors between birds foraging in flocks versus those foraging alone or they actually did worse when they foraged in flocks. Although foraging in flocks may not have directly benefited darker species, they may have decreased search time between food patches, increased the likelihood of foraging in beneficial locations, or decreased the risk of obtaining no food and increased energy consumption. For these species, finding prey is the challenge and these species may offset the cost of flock feeding by decreasing their time searching for food.

In summary, at ANWR, the model suggested that competition was an important process structuring the community. When I examined habitat use in both chapters II and II, I found that species of the same size tended to have high overlap in habitat use This pattern held for almost all sites. Examples included high overlap in habitat use between Great Egrets and Great Blue Herons at ANWR, MIWR and CNWR; and high overlap in habitat use between White Ibis and Tricolored Herons at MINWR. The only site in which there was an exception was LANWR, where the highest overlap occurred between Great Egrets and Reddish Egrets, both using lagoons more often than expected.

Limiting similarity predicts that species which have high overlap on one resource axis tend to have lower overlap on another resource axis. In chapter IV, I compared foraging behavior of birds in flocks versus those foraging solitarily and found that Great Egrets were more likely to be found in flocks versus Great Blue Herons and they were also more successful when foraging in flocks than Great Blue Herons. Perhaps this is an axis along which Great Egrets and Great Blue Herons partition resources. I.e., although they both use similar feeding habitat, Great Egrets are more likely to be found in these habitats when other birds are present and Great Blue Herons use it when primarily when they are alone. Other researchers have shown that these two species also partition resources based on prey characteristics including prey size (Great Egrets tend to eat smaller fish than Great Blue Herons) and by prey type.

For other species with high overlap in habitat use, such as the White Ibis and Tricolored Herons at MINWR feeding behavior is an important factors separating these species. White Ibis are primarily tactile feeders, whereas Tricolored Herons are visual feeders. As a result, they encounter different types of prey, which leads to another axis on which to partition resources. In this study, I did not examine diets of wintering wading birds, but this is an area that could be explored in the future.

One aspect that also deserves further study is the interaction of migratory versus resident wading birds. An intensive banding program followed by behavioral studies could examine questions of how the influx of migratory birds affects resident birds in terms of their habitat use, prey items, etc. If birds were marked with satellite transmitters, it could be determined where wading birds are foraging when they are not feeding on the island. There were several instances during the course of my research when it was difficult to locate the birds at MINWR and I suspected the birds had moved to the mainland to feed. A study of this nature could identify more details of important habitats used by wintering wading birds.

Another project which would enhance our knowledge of wintering wading birds would be to use GIS to quantify the availability of habitat types. This would allow for a direct comparison between habitat types used by wading birds versus habitat types available to wading birds.

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